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AN ECOLOGIC STUDY OF THE FLORA OF MOUNTAINOUS NORTH CAROLINA.

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TOPOGRAPHY.

THE mountain region of North Carolina is not a unit, dominated by a single range or group of mountains, but is a complex containing several features of nearly equal topographic importance. These are (1) the Blue Ridge, (2) the eastern Monadnocks and Piedmont valleys, (3) the Unaka Range, (4) the central mountain groups and intermontane valleys.[1]

The Blue Ridge.—The Blue Ridge may be regarded as forming the extreme eastern range of the Appalachian Mountains, carrying the main divide between the Atlantic and Gulf drainage. It reaches its greatest height in Grandfather Mountain, with an altitude of 5,964^{ft} (1,817^{m}). Three other peaks reach above 5,000^{ft} (1,525^{m}), and a dozen or more, most of them in North Carolina, are above 4,000^{ft} (1,220^{m}). The most striking topographic feature of the Blue Ridge is the great difference in slopes on its opposite sides, for it is steep on the eastern and gradual on the western slopes. The eastward-flowing streams have cut back into the mountain belt, and, having the advantage of a more direct course to the sea, have encroached upon the territory of the westward-flowing streams, and have robbed them of portions of their drainage basins.

The eastern Monadnocks and Piedmont Valleys.—The eastern Monadnocks form several groups of mountains along the extreme

[1] HAYES, C. WILLIS, The Southern Appalachians. National Geographic Magazine 1:319.

eastern border of the mountain belt, which have been more or less completely isolated by the erosion of eastward-flowing streams. The most important are the Brushy, South, and Saluda Mountains.

The Unaka Range.—The Unaka Range may be divided into a northern and a southern division. The northern division unites in the region of Grandfather Mountain with the Blue Ridge. From this point due west sixty miles (96^{km}), an irregular mountain mass extends to Paint Rock on the French Broad River. Compared with the Blue Ridge, the Unaka Range reaches a considerably greater average altitude, and contains most of the higher peaks in the southern Appalachians. Not only are these mountains higher, but their slopes are steeper, and their outlines more angular and rugged. The Unakas are equally steep on both sides, and slopes with a descent from crest to stream of 4,000^{ft} (1,220^{m}) are not uncommon. Many spurs leave the central chain, and between them are deep V-shaped ravines.

Central mountain groups and valleys.—From a commanding position somewhere on the Unaka Range, there may be seen stretching to the east and south a confused aggregation of peaks, ridges, and domes. The cultivated valleys are generally hidden from view, and, except for an occasional clearing and the grassy "balds" on a few of the higher domes, the whole region appears to be covered with a forest mantle. The interior mountains rise to considerable elevations. A very large number of summits reach altitudes between 4,000 and 5,000^{ft} (1,220–1,525^{m}), and a few culminate above 6,000^{ft} (1,825^{m}). The Black Mountains contain the highest peaks of the Appalachian Mountains, and from Roan Mountain they appear as a huge elongated range, broken into elevated domes, while the range culminates in Mount Mitchell, 6,711^{ft} (2,045^{m}), the highest point east of the Mississippi and 425^{ft} (130^{m}) higher than Mount Washington. Between these groups, and forming a sort of platform above which they arise, are many broad valleys, commonest toward the head of the streams. Only the smaller streams are flowing at the level of these valleys. Down-stream toward the northwest the broad valleys are found to be more and more deeply cut, until

these occupy deep narrow gorges. The broad valleys must have been formed at base level, before the commencement of the gorge cutting, and they afford the best possible evidence that the altitude of the region in which they are found has been increased by elevation in comparatively recent times.

HYDROGRAPHY.

The waters falling upon the several parts of this future National Park find their way eastward to the Atlantic, or southward directly to the Gulf of Mexico, or to the Mississippi River and thence to the Gulf. The divide between the Atlantic and Gulf drainage follows the crest of the Blue Ridge. The eastward-flowing streams are pressing this divide gradually westward by the capture of territory from less favorably situated streams west of the divide. Northwest of the divide the streams flow at first in the high broad valleys, then in deepening channels, directly to the higher, more rugged Unakas, which they cut through in narrow gorges, emerging upon the Appalachian Valley, those south of New River draining their waters into the Tennessee River.[2]

PHYSIOGRAPHY AND GEOLOGY.

The history of this region, as far as it concerns this paper, begins with the Cretaceous period. At least two great cycles of erosion are recorded in the southern Appalachians, in which the surface of an old continent was worn down from a considerable altitude nearly to base level. Shortly after the close of the Carboniferous period, the entire southern Appalachian province was finally lifted above sea level, and its subsequent history is recorded in the land forms. Following this uplift was a long period, during which the region was subjected to the physiographic processes constituting gradation. Finally, toward the close of the Cretaceous period, the whole province was reduced to a nearly featureless plain, the Cumberland peneplain, relieved

[2] See Hydrography of the southern Appalachian Mountain region. Water Supply and Irrigation Papers. U. S. Geological Survey, nos. 62 and 63. 8vo, 190 pages. Washington. 1902. These two papers by Henry A. Pressey give systematic measurements of the streams in the southern Appalachian Mountain district, and other data of special interest to the ecologist.

only by a few groups of hills where the highest mountains now stand. After the processes of base leveling were nearly completed, that is, toward the close of the Cretaceous period, the region was again uplifted, but unequally, so that at the same time its surface was warped. The streams had become sluggish, but the effect of the uplift was to stimulate them to renewed activity,[3] so that they began cutting upon the last-formed peneplain, a process in which they are still engaged.

PHYSIOGRAPHIC CHANGES INFLUENCING THE DISTRIBUTION OF PLANTS.

Constant change must have taken place in the flora, through the physiographic shifts in the continent, which have been described as taking place in the region of the southern Appalachians. New species were appearing by the process of mutation. Other species were crowded for room by the change of level and the wearing away of strata to which they had adapted themselves, for "if we suppose that the earlier Mesozoic uplands were the seat of the existing dicotyledons, then by the lowering of the surface by gradual consumption of the interstream areas, these forms must have been brought into conflict with the ancient flora of the lowlands and thereby forced into a contest for supremacy."[4] These changes in the physical condition of whole areas produced coincident changes in the constituent plants of the several ecologic regions. Xerophytes were replaced by mesophytes; mesophytes, by the wearing away of the soil and the formation of cliffs by xerophytes. Hydrophytes replaced mesophytes when an area became too wet for the tenancy of ordinary plants. Mesophytes replaced hydrophytes, as a lake area was robbed of its water by some newly encroaching stream. All of these changes were represented in the mountain region of North Carolina, and the plants involved in the readjustment to altered conditions were Cretaceous or Tertiary plants. With the development of the Cumberland peneplain, the forest covering, if one existed at that time (and we have no reason for

[3] HAYES, The southern Appalachians, *loc. cit.* 330.

[4] WOODWORTH, J. B., The relation between base leveling and organic evolution. The American Geologist **14**: 231.

believing that a heavy forest did not exist at that early date), was a mesophytic one with the addition of representative herbaceous plants that have not been preserved.

With the uplift of this plain, followed by its planing down by streams, valleys and gorges were created, and rocky strata were exposed, which supported, as such physiographic formations support today, a xerophytic flora. The character of the rocky outcrop influences the particular kind of vegetation, so that we may have a different flora with the same exposure of light, heat, and moisture, if the rocky formations are different. This does not depend so much upon the chemical composition of two different strata, as shown by Cowles,[5] but it is because one formation is further along in its life-history than is the other, so that the vegetation of the clay hill today may be seen on a sand hill in the future. With the widening out of the valley by erosion, and the slackening of the flow of any stream by the reduction of the elevations to base level, the xerophytes of the hillsides will be replaced by the mesophytes of the peneplain. The laws that control changes in the plant covering of a country are, therefore, plainly physiographic and edaphic, if the meteorologic conditions remain the same. We may have broad flood plains, hills, cañons, lakes, and swamps, depending upon the history of the ever-changing topography. Wherever hills are being eroded, rivers widened, waterfalls eliminated, lakes filled, or coastal plains enlarged, there is found a constant change in the plant societies, or a succession in definite order of plant groups. In any land which has undergone degradation from a mountainous topography to a peneplain, we ought to find a marked change in the organisms at the close of the cycle of denudation. In the first stages of change from original constructional topography, effects will be discernible. Sculptured slopes with ravines, sharp divides, and peaks cradle species and varieties by barriers which oppose ingress and egress.

In the progress toward final base leveling, the repeated diversion of the streams, or the reversals of drainage, are a constant

[5] COWLES, H. C., The influence of underlying rocks on the character of the vegetation. Bulletin American Bureau of Geography **2**:— [pp. 26]. Je and D 1901.

cause of changed conditions which Alfred Russell Wallace emphasizes as of importance in the modification of species.[6] The cycle begins in a mountainous tract with least facility for migration of species, and ends in broad lowlands, which favor the easy migration and wide distribution of plants and animals.[7]

The distribution of plants in the region of the southern Appalachians demonstrates the above-mentioned facts. Kearney[8] has called attention to the presence of a Lower Austral (austro-riparian) element in the flora of the mountains of North Carolina. Over one hundred species, which are most abundant and most widely distributed in the austro-riparian area, are known to occur in the mountains at an elevation of 1,000^{ft} (300^{m}) or more. Below that altitude the flora of the southern Appalachian region is mainly Carolinian, and the presence in its midst of numerous austro-riparian forms would be expected. The occurrence, however, of Lower Austral species at higher elevations in the midst of a chiefly transition flora is the noteworthy fact in the distribution of plants in the southern Appalachians. In studying this flora, one soon reaches the conclusion that it comprises two categories of species, which are markedly different, not only in their systematic relationships, present distribution, and past history, but even to a considerable degree in their ecologic constitution. Two types of plants may be distinguished: those of neotropic origin, which have in all likelihood made their first appearance in the Appalachian region in geologically very modern times, probably after the close of the glacial epoch; and those not of neotropic origin, which probably represent the more or less modified descendants of the flora that in later Eocene or Miocene time extended to high northern latitudes, represented in eastern North America by two closely allied species, one in the coastal plain, and the other in the Appalachian region.

In order to explain the facts in the case, botanists have had

[6] WALLACE, A. R., Darwinism, chap. v.

[7] WOODWORTH, J. D., The relation between base leveling and organic evolution. The American Geologist **14**:217. 1894.

[8] KEARNEY, The lower austral element in the flora of the southern Appalachian region. Science N. S. **12**:831.

recourse to the movement of glaciers southward during the ice age. It appears to the writer that the alternation of cold and warm periods is not necessary to account for the facts described above. An attempt is made in what follows to outline an alternative hypothesis which appears to be a more satisfactory exposition of the case. The elevation of the southern Appalachian region from the Cumberland base level satisfactorily accounts for the differentiation of the corresponding mountain and coastal species. The species now found on the mountains adapted themselves to the higher elevations, and, being more plastic, were wrought upon by the forces which were and are at work in the gradation of the southern Appalachian region. For no fact in biology is better known than the capacity of some species to endure a wide range of physical conditions, while others are fatally sensitive to comparatively slight differences of environment. The modification of the species above mentioned was influenced by the rapid change in the physiography and topography of the country, and not by the glacial ice-sheet, which during a late geologic epoch covered the whole of North America. The oscillations of level are known to have taken place, and it is conceivable that the progenitors of the austroriparian plants of the mountains and coastal plain, specifically identical, mingled when the country was a level peneplain, becoming differentiated as the elevation of the land became more marked. The distribution of plants which represent the characteristic flora of Eocene and Miocene times is thus accounted for.

We have then, in the physiographic changes which have taken place in this mountain region, an explanation of the peculiarities of the flora of the southern Appalachians, which displays certain anomalies of distribution and isolation of monotypic plants. The presence of *Hudsonia montana* Nutt. on the summit of Table Rock is thus explained.[9] Table Rock is an undenuded remnant of a former peneplain, and it is likely that *Hudsonia montana* Nutt. was once more extended in its distribution, but has been isolated by the erosion of the larger part of the plain on which it formerly grew in abundance. *Dicentra*

[9] Collected there by Dr. John K. Small.

eximia DC. is another illustration, growing in a rather restricted area in the Doe River Gorge, where the river cuts between Iron Mountain and Gap Creek Mountain, North Carolina. *Shortia galacifolia* Torr. & Gray, *Lilium Grayi* S. Wats. on Roan Mountain, *Buckleya distichophylla* Torr. on Paint Rock are examples of this same local distribution and isolation.

PHENOLOGIC DISTRIBUTION OF PLANTS.

Four kinds of plants with reference to their phenologic distribution may be distinguished in the vegetation of the forests of eastern North America; viz.: plants of boreal genera (Arctic, Hudsonian, Canadian species), plants of temperate genera (Alleghanian and Carolinian), plants of warmer temperate climate (austro-riparian), and neotropic genera.

Both boreal and temperate species bloom in the spring before they are shaded by the leafing trees, but for different reasons. The plants of temperate origin vegetate and blossom in the spring before the trees are in leaf, because, as a matter of light relationship, it is the only season in which the functions of these plants can be performed adequately, and this presupposes the influence of a certain number of heat units greater than for boreal species and less than for those of more southern origin. A more detailed statement on this subject will be made subsequently. The boreal plants, however, of the eastern Appalachian forests, blossom and vegetate early in the season, because that is the part of the year at which the development of these species, which require a minimum of heat units, is most adequately performed.[10] The writer has shown this in a detailed manner in a paper published in *Science*.[11] The Scandinavian element of our flora consists of plants which mature their seeds quickly before the summer is well advanced. This marks them

[10] The presence of many boreal plants in the forests and peat bogs of the northern states is accounted for by the encroachment of tree vegetation, after the glacial epoch, upon the areas occupied by the boreal plants, which surrounded by the trees, were destroyed or compelled to grow during the period when the trees are leafless. The movement of trees northward was occasioned by the fact that the land area, left bare by the retreat of the glaciers, was one of low tension, while the country to the south, as we have seen, was one of high tension.

[11] HARSHBERGER, The origin of our vernal flora. Science N. S. 1:92–98. Ja 25. 1895.

as physiologically adapted to the influences of a previous short glacial summer. This rapid growth is insured by the activities of the plant during the previous short season in storing up large amounts of reserve material for the next brief season's growth. Even under favorable conditions of summer heat, every external perceptible vital motion in these boreal plants ceases, and it is only after a dormant period of some months, that growth can commence anew. This periodic alternation of vegetative activity and rest is in general so regulated that for a given species of plant both occur at definite times of the year, leading to the inference that the periodicity only depends upon the alternation of the seasons, and, therefore, chiefly upon that of temperature and moisture. The plants of Scandinavian affinity agree physiologically in having a periodic growth and rest. The following diagrams will illustrate this. Diagram *B*, if compared with diagram *A*, shows that the period of vegetative activity of our spring plants of boreal origin corresponds with an arctic or glacial summer, while the dormant period corresponds with an arctic winter, although our present summer has encroached on the former glacial winter.

A. Astronomical Year during Glacial Period.

Vegetative Period	Flowering and Reproductive Period	Dormant Period
Growing Period of Plants		
Arctic Summer		Arctic Winter

B. Astronomical Year — 1903.

Vegetation	Flowers	Dormant Period	
Growing Period of Boreal Plants		Dormancy of Summer ← →	Dormancy of Winter
Present Summer			Present Winter

The plants of warmer temperate climate (austro-riparian species) require a greater number of heat units than those plants just described, and their distribution at present depends largely upon temperature and soil conditions. In the case of the austro-riparian species found in the southern Appalachian mountains, two factors are probably most effective in permitting these species to maintain themselves in what would seem to be an unfriendly environment, viz., amount of insolation and the nature of the soil.[12]

A favorite situation in the mountains for colonies of lower austral species is on the southern exposure of hills, where the angle of inclination and the position with reference to the sun insure the greatest possible amount of insolation. The soil preferred by the great majority of these species is light, sandy, and poor in organic material; it is consequently readily permeable to water and becomes quickly and strongly heated, being thus similar to the soils which cover a great part of the coastal plain.

Unfortunately no phenologic data are at hand with reference to the plants of warmer temperate character. In lieu of exact data, a reference to Chapman's *Flora*[13] may assist in determining the position of these plants with reference to the period of flowering. Those plants not of neotropic origin, which are probably the more or less modified descendants of that characteristic flora which existed in Eocene and Miocene times, and species of genera that appear to be on the wane, blossom in general, according to Chapman, from May to July, and are not looked upon as spring plants, which blossom from March until May. The neotropic element in the flora of the eastern United States is represented by plants that bloom in general from June until October,[14] and are therefore summer and autumn species. This result of a phenologic tabulation of the austro-riparian plants might have been expected, when the origin and physio-

[12] KEARNEY, *loc. cit.* 841.

[13] CHAPMAN, Flora of the southern United States. 3d ed.

[14] Another group of plants, derived like the Cactaceae and Compositae from the southwest, bloom at about the same period as the plants of neotropic origin. See my paper in Science, *loc. cit.*

logic constitution of these plants is taken into consideration; for, according to the laws of temperature control of plants, species of neotropic and warm temperate origin need a large sum of heat units to carry on adequately their life-processes, and these are not properly carried on unless the specific number of heat units is provided in the environment.

INFLUENCE OF GLACIERS ON THE FLORA OF NORTH CAROLINA.

Upon the retreat of the ice-sheet, that portion of the continent north of the terminal moraine was tenanted again by plants that migrated northward, which as species were adapted to a cold temperate climate. A large number of these species came from the southern Appalachians and adjoining regions, where they had remained undisturbed in their original haunts during the long ice age, and were in a plastic condition for growth in a new environment, through the influence of the pressure of species upon each other in their southern home, and through the physiographic vicissitudes to which these fictile forms were subjected. Many species, therefore, growing in the North Carolina mountains, found congenial conditions in the more extensive land areas in the north.

An inspection of the forest maps to be found in the ninth volume of the Tenth Census Report, *Forest Trees of North America*, will show that there is a center of distribution which comprehends the area of the present states of southern and central Pennsylvania, West Virginia, Kentucky, Tennessee, western North Carolina, southwestern Virginia, northern Georgia, Alabama, Mississippi, where the largest number of species of the most important genera of North American deciduous trees will be found. A study of these maps reveals an important fact, that the spread of the species from this common center has been in a series of more or less concentric waves. Three waves may be distinguished. The first wave consisted of the distinctly glacial flora, which skirted the border of the ice-sheet. The second consisted of the present boreal forms, and the third was a wave of deciduous shrubs and trees, oaks, hickories, and a host of others. The species most successfully provided with means of distribution and most easily adjustable extended furthest

from the original home after the glacial epoch, which circumscribed the area of the original dense forest of the Miocene period. The outer confines of any particular genus is usually occupied, as shown in the maps, by a single species. Nearer the center two species are found; still nearer, if the genus is a large one, three, and still nearer four, etc. The position of the various shades of green on the maps suggests the circles of impulse produced when a stone is thrown into a basin of water. Theoretically these waves spread circumferentially in all directions, unless they meet with obstacles, when they are deflected. Similarly, the maps suggest a series of distributional impulses, by which the various species of oaks, ashes, hickories, and chestnuts were forced out from a parent forest of great density into the area left bare by the retreat of the great ice-sheet. The force which impelled this migration outward from the original forest, a relict of the continental forest of Miocene times, was the tension produced by the species associated together and in a struggle for supremacy, as regards room, light, etc. This struggle for existence must have been intense, as evidenced by the great size, height, and straightness of bole of the deciduous forest trees. Only two alternatives were left the species composing this original forest, namely, extinction or migration. Fortunately for the forest, an area of little or no tension was opened up upon the retreat of the glacial ice. The migration from an area of great tension has been and always will be toward an area of little tension.

MacMillan[15] remarks on this point, with reference to the character of the Minnesota flora, that it has been shown that, while the valley of the Minnesota is geographically central, it is by no means botanically central, but, on the contrary, strongly southern and eastern. Bessey[16] has shown that the trees and shrubs of Nebraska have come up the Missouri bottoms and spread from the southeastern corner of the state west and northwest. Mason states that the trees of Kansas show the same

[15] MACMILLAN, The Metaspermae of the Minnesota Valley 758, 759. 1892.

[16] BESSEY, The forests and forest trees of Nebraska. Ann. Rep. State Bd. of Agric. 1899: 79–102.

origin. Adams[17] has demonstrated this clearly in a study of the faunal distribution of animals and in a cursory way with plants.

The marshaling of these facts exhibits the flora of the southern Appalachians and of the mountains of North Carolina in a new light. That the plants of the northeastern and north central United States (except those left as high northern plants on the nunataks and non-glaciated islands and those of cold temperate habit) are derived from the region of the southern Appalachians, adds considerable zest to the study of the flora of these elevated mountain lands.

PRINCIPLES UNDERLYING THE DISTRIBUTION OF PLANTS IN EASTERN AMERICA.

It is advisable at this point to make a restatement of the principles underlying the distribution of plants in eastern America. These statements are derived from the work done by Gray, Hooker, and others on the distribution of North American plants, with additional facts which seem to the writer necessary to mention because of recent work that has been published with reference to the flora of North America in general.

1. Subsequent to the great Cretaceous uplift in a favorable period of mutation, the north temperate regions of Europe, Asia, and America which extended to high northern latitudes became the habitat of dicotyledons and monocotyledons identical as species in most important points.

This region was occupied by a forest of great density,[18] composed of numerous species of trees, shrubs, and herbaceous plants, and these plants were subsequently definitely allocated during preglacial times to certain geographic areas by the planing down of the country to base level.

3. The movement of the glaciers southward over the north-

[17] ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of flora and fauna. Biological Bulletin **3**: 115–129. Jl 1902.

[18] GRAY, ASA, Sequoia and its history. Proceedings American Association Advancement of Science **21**: 1. 1872. Scientific papers of ASA GRAY **2**: 142; also *ibid.* **2**: 204. *Cf.* GRAY, Forest geography and archæology. American Journal of Science **16**: 85–94; 183–194.

land exterminated the plants of preglacial times without forcing a migration southward, except the northern herbs and trees left on the moraines, unglaciated islands, glacier margins, and nunataks of the great ice field.[19]

4. During the late Pleistocene, and also during the interglacial period, the Scandinavian element of the boreal and north temperate floras was introduced by the migration of plants from Scandinavia by the high northern roadway through northern Europe and Asia to North America, and, as shown, these plants remained on the retreat of the glaciers in the far north, and on the alpine summits of the more elevated mountains, or were held trapped in the cool shade of the north temperate forest or isolated in cold sphagnum bogs.

5. The plants of this north temperate region south of the terminal moraine during glacial times remained, on the retreat of the glaciers, in undisturbed possession of their original habitats. During the ice age they were still further reduced in numbers and influenced in their distribution by the physiographic forces constantly at work in the shaping of the continent.

6. Upon the retreat of the ice-sheet the glaciated area was supplied with plants from two main sources: (*a*) the plants that had maintained themselves in the north during the ice age, and (*b*) the contingent of plants supplied by the territory to the south and east.

7. Conclusively, therefore, the facts indicate the absence of a southern migration of plants.[20] Rather, they point to the glaciers as the important factor in the isolation of such botanic regions as eastern North America and eastern Asia, which perforce show affinities in their floral make-up that can be explained only by reference to the principles aforementioned.

[19] WRIGHT and UPHAM, Greenland icefields and life in the north Atlantic 197–198. 1896.

RUSSELL, Glaciers of North America 86 and 117. 1897; also in Annual Report U. S. Geological Survey **13**: 19–21. 1891–92.

WRIGHT, G. FREDERICK, The ice age in North America 57–62. 1891; also American Geologist **8**: 330.

[20] This southern migration seems to the writer well-nigh impossible, because it would mean a movement from an area of lower tension to one of higher tension.

8. Following the glacial period the modification of the plants left in the several widely removed continental areas, eastern North America and eastern Asia, became accentuated, as time elapsed, until the similarities which are marked in the plants of preglacial times became less well defined and the differences evident in the two floras become the feature of recent times.

9. These facts argue for a great antiquity of the flora of the mountains of western North Caroliua. The presence of so many peculiar types of plants, not found elsewhere in America and having their closest relatives in eastern Asia, makes it more certain that groups, now broken up and detached, were once continuous, and that fragmentary groups and isolated forms are but the relics of widespread types, which have been preserved in a few localities where the physical conditions were especially favorable, or where organic competition was less severe.

This important principle is evidenced on every hand as a botanist travels through western North Carolina. The large size of the trees, the close commingling in a dense forest of a great variety of species, the graded-down appearance of the land surface, and the rounded contour of the mountains, all impress the fact upon him that the country through which he travels has been subjected through long ages to the continued action of climatic forces which have carved the land into its present form and influenced the character of the vegetal covering. This impression is greatly heightened, if the following nine criteria for determining the centers of dispersal are applied to the study of the region in question:[21]

1. Location of greatest differentiation of type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.
4. Location of maximum size of individuals.
5. Location of greatest productiveness and its relative stability.
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations, or modi-

[21] ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of fauna and flora. Biological Bulletin 3: 122.

fications radiating from the center of origin along the highways of dispersal.

9. Direction indicated by biogeographic affinities.

EDAPHIC FACTORS DETERMINING THE CHARACTER OF THE FLORA OF WESTERN NORTH CAROLINA.

The soils of the higher mountains are rather fine and even-grained loams, gray or red in color, or black from organic ingredients; the loamy and generally stiffer subsoils are red or gray. Over the larger part of the area they are derived from the decomposition, *in situ*, of gneiss or gneissic schists, and are sufficiently deep for tree growth, particularly along the lower slopes. In portions of the region the soil derived from slates, quartzite, and metamorphosed sandstones are shallower, thinner, and not so favorable to tree growth.[22] Soil, according to the definition of Professor Dokouchayev, a Russian investigator, is the superficial horizon of rocks in which the general processes and phenomena of weathering, transportation of particles, etc., combine with the biologic processes due to the influence of plants (lichens and alpine plants), animals, and micro-organisms, such as nitrifying bacteria.[23] A forest soil, such as we find in western North Carolina, is an expression, therefore, not only of the physico-geographic, geographic, and geophysic forces which have been brought to bear in its formation, but also of the geobiologic forces which have been at play. A study of any soil cannot fail to reveal many peculiarities of the vegetation that covers it, but it also throws a flood of light upon the succession of floras which may have flourished at any particular time in a given region. To elucidate: the soils of a given territory are influenced by the life-activities (instance the Leguminosae) and the dead remains of plants and other organisms (peat beds, humic compounds, animal manures, guano, etc.). The soil also influences the

[22] PINCHOT and ASHE, Timber trees and forests of North Carolina. N. C. Geol. Surv. Bull. **6**: 220. 1897.

[23] SIBIRTZEV, N., Genetic classification of soils. Zapiski Novo-Alexand. Inst. Selsk. Khoz. Lyesov. Memoirs of the Institute of Agriculture and Forestry at Novo Alexandria, Government of Lublin 9^2: 1–23. 1895. *Ibid.*, 11^3: 1–4. 1898. Experiment Station Record **12**: 705.

development and the life-activity of these organisms and their decomposition after death. The character of the plant growth, for example, plays not only a direct, but an intermediate rôle in the formation of soil. The relief of the soil has an important influence in determining the drainage, temperature, etc. And lastly, the successive changes which have taken place in the climate, the encroachments of the forests, the spread of marshes, the drying up of the soil, etc., must in their turn influence the character of soils. A knowledge of the laws and the forms of these influences makes it possible to obtain from the study of soils a basis for the reconstitution of the recent past of the country and for sketching its recent geophysic and geobiologic history. An inspection of the soils of western North Carolina reveals a close relationship between the vegetal covering and the soil. There are a number of humus dwellers with ectotrophic and endotrophic mycorhiza. Such plants as the oaks, beeches, chestnuts, poplars, willows, pines, spruces, and firs are provided with ectotrophic mycorhiza and therefore are to a certain extent dependent on the humus of the soil. Without it a dense forest could not exist, and in any region, such as the mountainous area of North Carolina, the luxuriance of the forest is a correlative of the richness of the soil in humus and its mechanical condition, and *vice versa*.[24] Plants with endotrophic mycorhiza also add their quota to the upbuilding and maintenance of the forest litter, and so do many fungi. In North Carolina, as elsewhere, the rotten windfalls and the fallen leaves return many valuable ingredients to the earth. In the North Carolina mountains, if undisturbed by man, a deep soil rich in organic detritus is found, and this clearly points to the long occupation of the territory by dense forests.

These introductory remarks have been made to show the delicate balance which exists between the vegetation of western North Carolina, on the one hand, and the soil and physiographic features, on the other. Constant change has been manifested in

[24] Another indication of a soil rich in humus is a great variety of saprophytic fungi belonging to several well-recognized groups, such as the Polyporei, Agaricineae, etc.

the transformation that has been made from the monotonous plateau of early Cretaceous times, covered with a rather tame flora, to the richly diversified configuration of the mountains and plains of today, clothed with the most magnificent forests (excepting those of the Pacific slope) to be found anywhere in the western hemisphere. The ecologic disposition of the vegetation with reference to the topography next concerns us.

[*To be concluded.*]

A SKETCH OF THE FLORA OF SOUTHERN CALIFORNIA.

S. B. PARISH.

(*Concluded from p. 222.*)

THE CISMONTANE AREA.

THE genera which are confined to this area are more in number than the distinctive genera of both the other areas combined. Some of them have so wide a range as to deprive them of any but the most general phytogeographical value, and these are omitted from the following table. I have designated by an asterisk those genera which are represented by species that come to us from the south; the others are of northern affinity, and, with the exception of a few belonging to the central valley of California, are plants of the Pacific coast flora.

DISTINCTIVE GENERA OF THE CISMONTANE AREA.

Interior Subregion	Coastal Subarea	Common to Both Subareas	
Fimbristylis	*Acalypha	Adenostoma	Eremocarpus
Githopsis	Achyrachaena	Alchemilla	Godetia
*Imperata	Arbutus	Amorpha	Heterotheca
Juglans	Boykinia	Apiastrum	Heteromeles
Koelia	Calamintha	Athysanus	Loeflingia
Lagophylla	*Cneoridium	Baeria	Mecanopsis
Phragmites	*Cupressus	Cardamine	Oenanthe
*Schoenus	Eryngium	Caucalis	Palmerella
Umbellularia	Grindelia	Chlorogalum	Papaver
	*Harpagonella	*Conyza	Pickeringia
	Micromeria	Corethrogyne	Platystigma
	Myrica	Datisca	Platanus
	*Oxalis	Dendromecon	Scrophularia
	Sphacele	Dentaria	Tropidocarpum
		Dicentra	Valerianella

From a study of the distribution of the avifauna of California[24] Mr. Charles E. Kellar was led to propose a transitional area to embrace a strip of territory from the Coast Mountains, and including them, to the sea; and extending from Monterey

[24] KELLAR, CHAS. E., Geographical distribution of land birds in California. Zoe 1: 296, and map.

into Lower California. This area is characterized by the presence of forms from the Pacific coast, the Californian and the Sonoran areas, as these are laid down by Dr. Merriam.[25] The same conclusion is reached by a consideration of the floral distribution of the region. In its upper portion genera and species which are distinctively of the northern coast flora are both numerous and abundant; passing southward these become fewer and rarer. Many entirely fail to reach our part of this area, while others, like *Myrica Californica* and *Arbutus Menziesii*, are here local varieties. On the other hand, distinctively Sonoran plants, such as the yuccas and the Cactaceae, common in the south, drop out as one passes northward. At no point can a dividing line be drawn; and there is an important element of the flora, in considerable part connecting it with that of the Californian area, which is about equally abundant throughout the whole region.

The table last given, of genera exclusively Cismontane, shows but a weak Sonoran element, and from it one might infer that the flora of this area was overwhelmingly Coastal and Californian. But the table exhibits only half the truth, since the Sonoran element is represented mostly by genera which the Cismontane area shares with the Desert. Indeed, so prevalent is this element that it gives the flora an aspect decidedly Sonoran. The abundance of yuccas and the large development of the Cactaceae have been mentioned already. Some other desert plants that pass into the Cismontane are *Prosopis juliflora*, *Bebbia juncea*, *Philibertia linearis*, *Chilopsis saligna*, *Abronia villosa*, *Encelia farinosa*, *E. Californica*, *Viguiera deltoidea* var., etc. Omitting species that merely enter the respective borders of one area or the other through the different passes, there are over forty species of the Desert fairly frequent throughout the Cismontane, or a considerable part of it; on the other hand, hardly a single distinctively Cismontane species more than enters the confines of the Desert.

A small group of plants, which have entered directly from Lower California, inhabit a narrow strip along the coast. Some barely pass our borders; few penetrate very far within it, and

[25] MERRIAM, J. HART, N. Am. Fauna 3, map 5.

the last one disappears at Santa Barbara. They are enumerated below.

PENINSULAR SPECIES ALONG THE COAST.

Acalypha Californica	Cneoridium Californicum	Mamillaria dioica
Agave Shawii	Dithyrea Californica	Opuntia prolifera
Arctostaphylos diversifolia	Frankenia Palmeri	Opuntia serpentina
Baccharis sarothroides	Isomeris arborea	Simmonsia Californica
Beloperone Californica	Iva Haysiana	Viguiera laciniata
Cereus Emoryi		

The Cismontane area comprises two fairly distinct subareas. These probably owe the differences of their floras to the fact that one is more exposed than the other to the fogs and humid air of the ocean. The line separating them follows those elevations which intercept the direct action of these influences; namely, the seaward flanks of the Cuyamaca and Palomar Mountains, the Temecula Range, and the lower hills which continue it beyond the Santa Ana River.

The district between this line and the Pacific Ocean may be called the Coastal subarea; that between this line and the San Bernardino Range constitutes the Interior subarea. The latter subarea includes the San Fernando, San Bernardino, and San Jacinto Valleys. Where the wide Los Angeles Valley opens out to the sea the two subareas coalesce, and some of the most characteristic Coastal species are carried inland to the base of the San Gabriel Mountains.

The most evident characteristic of the Coastal subarea is the prevalence of oaks. Its rolling hills are covered commonly with open groves of *Quercus Engelmanni* and *Quercus agrifolia;* indeed, the first of these oaks and *Rhus laurina* may be considered the characteristic arboreal plants of this subarea. Its chaparral is much more largely composed of scrub-oak, mostly *Quercus dumosa*, than that of the Interior, where *Adenostoma fasciculatum* is the principal shrub. But the Interior subarea differs from the Coastal mostly in a negative way; the latter possessing fully one hundred species which do not extend into the former. Among these are eight species of Atriplex, five each of Chorizanthe and Phacelia, four each of Gilia and Antirrhinum, and three each of Astragalus, Calochortus, Cotyledon, and Salvia.

The species which are restricted to the Interior subarea are comparatively few and unimportant. Some which contrast with Coastal species may be named.

SPECIES RESTRICTED RESPECTIVELY TO THE INTERIOR OR THE COASTAL SUBAREAS.

Interior Subarea	Coastal Subarea
Adiantum Capillus-Veneris	Adiantum emarginatum
Andropogon macrourus	Andropogon saccharoides
Antirrhinum glandulosum	Antirrhinum Nevinianum
Aplopappus linearifolius	Aplopappus ericoides
Artemisia Parishii	Artemisia Palmeri
Boykinia rotundifolia	Boykinia occidentalis
Calochortus Plummerae	Calochortus Weedii
—— splendens	—— Dunnii
Carex Barbarae	Carex spissa
Chorizanthe Fernandina	Chorizanthe laciniata
—— Parryi	—— fimbriata
Euphorbia ocellata	Euphorbia misera
Gilia Californica	Gilia floribunda
Helianthus Parishii	Helianthus Oliveri
Hemizonia Wrightii	Hemizonia virgata
Lathyrus laetiflorus	Lathyrus splendens
Monardella Pringlei	Monardella hypoleuca
Opuntia Bernardina	Opuntia prolifera
Phacelia Davidsonii, var.	Phacelia Douglasii
Ribes glutinosum	Ribes speciosum
Zauschneria Californica	Z. Californica microphylla

There are also certain plants that are confined to the immediate shores of the ocean, either on the sands of the beach, or in the tidal marshes or meadows that occur in some places. These are exhibited in the subjoined table.

LITTORAL PLANTS.

Arenicolous Species	Halophilous Species
Abronia maritima	Astragalus pycnostachys
—— umbellata	Atriplex hastata
Amblyopappus pusillus	Batis maritima
Aphanisma blitoides	Jaumea carnosa
Atriplex leucophylla	Juncus acutus, var.
—— microcarpa	Lasthenia Coulteri
Calandrinia maritima	Monanthochloe littoralis
Convolvulus Soldanella	Salicornia ambigua
Franseria bipinnatifida	—— herbacea
Mesembryanthemum aequilaterale	—— mucronata
—— crystallinum	Scirpus Tatora
—— nodiflorum	Spartina glabra
Oenothera viridescens	Statice Limonum, var.

THE INSULAR FLORA.

The islands of Santa Catalina and San Clemente, situated some twenty miles off the seacoast, have floras of great interest. They are parts of that general coast-island flora which has received no little attention, not only by reason of certain anomalous elements in its composition, but as well from the problems of origin and affinity to which these give rise.

It has been contended that the coast islands are the emergent peaks of a submerged continent, still retaining the vestiges of its peculiar vegetation. Emergent peaks they certainly are, but a more reasonable theory regards them as belonging, not to another continent, but to a chain of mountains paralleling the present Coast Range, now, save for them, sunk beneath the waters of the ocean, whose waves roll over what was once a broad valley separating the two ranges. Under this theory the peculiar insular plants, such as Lyonothamnus and the species of Lavatera, are to be regarded as the remnants of a flora, antedating the period of subsidence, once common to the whole coast region. Preserved by its isolation on the islands, it has perished on the main-land, or is, perhaps, still feebly represented by a few species, such as *Pinus Torreyana* and *Euphorbia misera*, which retain a precarious foothold along the coast.[26]

[26] The following papers will be found of interest to those desirous of studying the insular floras and their relationship and probable origin:

BRANDEGEE, T. S.—Convolvulus occidentalis. Zoe **1**: 85. Plants of Santa Catalina Island. Zoe **1**: 107. Flora of the Californian islands. Zoe **1**: 129. Lavatera—is it an introduced plant? Zoe **1**: 188. Flora of the Santa Barbara Islands. Proc. Cal. Acad. II. **1**: 201.

DAVIDSON, GEORGE.—The submerged valleys of the coast of California, U. S. A., and of Lower California, Mexico. Proc. Cal. Acad. III. Geo. **1**: no. 1.

GREENE, E. L.—Notes on the botany of Santa Cruz Island. Bull. Cal. Acad. **2**: 377. A botanical excursion to the island of San Miguel. Pittonia **1**: 74.

LE CONTE, JOSEPH.—The flora of the coast islands of California in relation to recent changes in physical geography. Bull. Cal. Acad. **2**: 377.

LYON, W. S.—The flora of our southwestern archipelago. BOT. GAZ. **11**: 197, 230.

PARISH, S. B.—The Pacific Lavateras. Zoe **1**: 300. Southern extension of the range of *Polypodium Scouleri*. Fern Bull. **9**: 40.

TRASK, BLANCHE.—Field notes from Santa Catalina Island. Erythea **7**: 128.

WATSON, S.—Flora of Guadalupe Island, Lower California. Proc. Am. Acad. **11**: 105.

YATES, L. G.—Stray notes on the geology of the Channel Islands. Rept. Cal. State Mineral. **9**: 171. Insular floras. *L. c.* 179.

The number of the endemic species of plants occurring on the coast islands was claimed, at one time, to be much larger than is admitted at present. Among them are the remarkable monotypic Lyonothamnus, and Lavatera, with four too closely allied species, no two of them found on the same island, a genus which is unrepresented elsewhere in the western world. All the other endemic insular species belong to genera which have representatives on the adjacent mainland. Probably less than thirty of these species are valid, and of these several are no more than robust developments of plants of the neighboring coast. Twelve of them are found on the islands off the Mexican coast, as well as on the Californian islands, so that hardly more than fifteen remain which are peculiar to the latter group.[27] In the subjoined list species endemic to Santa Catalina and San Clemente are in italic; species too closely connected with continental ones, perhaps mere varieties of them, are designated by an asterisk.

PLANTS OF SANTA CATALINA AND SAN CLEMENTE ISLANDS.

Astragalus Nevinii	Galium Catalinense	Lyonothamnus floribundus
*Ceanothus arboreus	Gilia Nevinii	Malacothrix foliosa
**Cercocarpus Traskae*	*Hemizonia Clementina*	—— insularis
*Crososoma Californica	Lavatera assurgentiflora	*Plantago dura*
*Eriogonum giganteum	*Phacelia Lyoni*	Quercus tomentella
Eriophyllum Nevinii		

These distinctively insular species constitute but an insignificant proportion, although a most interesting element, in the plant population of the islands, which, with these exceptions, is made up of species from the neighboring mainland. The islands are therefore to be considered as a subarea of the Cismontane area, and but slightly differentiated from the Coastal subarea.

PHYTOGEOGRAPHICAL DIVISIONS.

In accordance with the views set forth above, the life-areas of southern California are exhibited in the subjoined table. They are provisional merely, for not only does much remain to be learned of the distribution of our flora, but they are based on an examination of the flora alone, whereas the fauna and avifauna

[27] BRANDEGEE, T. S. Zoe 1: 129.

must also be taken into consideration. It is believed, however, that the divisions here laid down will not be greatly modified when all the facts bearing on the problem come to be known.

LIFE AREAS OF SOUTHERN CALIFORNIA.

Provinces	Regions		Areas	Subareas
Boreal	Arctic		Alpine	
	Boreal	Nevadan	Hudsonian	
			Canadian	
			Transition	Upper
				Lower
Sonoran	Lower Sonoran		Desert	Mojave
				Colorado
	Upper Sonoran		Cismontane	Interior
				Coastal
				Insular

The various life-zones in an ideal section across southern California, from the lowest point in the deserts, across the highest mountain peak, to the coast islands, are represented below:

IDEAL SECTIONAL DISPOSITION OF THE LIFE-ZONES.

Alpine	
Hudsonian	
Canadian	
Upper Transition	
Lower Transition	
Juniperus Zone	Pseudotsuga Zone
Piñon Zone	Interior Subarea
Yucca Zone	Coastal Subarea
Larrea Zone	Littoral Zone
Atriplex Zone (?)	Insular Subarea

INTERRELATIONS OF THE DIFFERENT LIFE-AREAS.

It is not to be understood that these various phytogeographical subdivisions are strictly limited and sharply defined, as they are represented on biological charts. Here, as always, nature does not pass with abruptness from one formation to another; rather one shades gradually into another. Thus we find few, if any, species where boundaries are strictly conterminous. And in passing across the country a successive and continuous disap-

pearance of species is observed, and the appearance of new ones in their places.

Under the varying influences of soil, moisture, exposure, wind currents,[28] and other subtler, and often unrecognizable, causes, adjoining zones interpenetrate and overlap each other in a most irregular manner. Nevertheless they have a real existence and evident boundaries, manifested by the general character of the vegetation. The most unobservant quickly notices the change from one kind of plant growth to a very different kind, as he passes from the Desert to the Nevadan or the Cismontane areas. The trained eye of the botanist notes in each the limits of several subareas, yet detects in each plants seen also in the others.

The interrelation of the floras of the several areas is manifested by the numerous genera which have representative species in each. Most of them show, by the larger number of species growing in it, the area where the conditions are best suited to their development, and, when the preference is well marked, that area may be considered the one to which they specially belong. Some of the larger of these genera are tabulated below:

INTERRELATIONS OF GENERA.

Genera	Species and Varieties			Genera	Species and Varieties		
	Nevadan	Cismontane	Desert		Nevadan	Cismontane	Desert
Allium	3	3	2	Gilia	11	29	19
Arabis	5	1	2	Hosackia	5	19	4
Astragalus	7	6	17	Juncus	6	5	1
Atriplex	0	10	7	Krynitzkia	1	6	11
Calochortus	1	9	3	Lupinus	9	16	3
Carex	23	10	1	Mimulus	10	11	2
Chaenactis	2	3	6	Phacelia	4	16	12
Chorizanthe	2	11	6	Plagiobothrys	1	6	1
Eriogonum	10	9	20	Pentstemon	5	8	6
Trifolium	2	15	0	Ranunculus	5	3	0

While most plants have a definite and often very restricted range, others are able to adapt themselves to such various environments that their limits are circumscribed by no narrower

[28] The influence of wind currents from the deserts is very potent in disturbing the life-zones in the narrow Nevadan belt; and in a similar manner the moist winds from the ocean modify the boundaries of the Interior and Coastal subareas.

boundaries than those of a biological province. Plants such as these are without phytogeographical value in the study of more limited areas. For an opposite reason plants which are very localized are likewise without value. Only those whose limits are neither too widely extended nor too restricted are serviceable to the phytogeographer in determining the biological subdivisions of a region. For this purpose trees and shrubs are more useful than humbler plants. Not only are they more readily observed, but their greater duration requires a closer adaptation to climatic conditions, while their stature and their depth of root render them less immediately dependent on conditions of pure locality, such as surface moisture or shelter.

PHYSIOGNOMIC CHARACTERISTICS OF THE FLORA.

The most striking feature of the southern Californian flora, taken as a whole, is the prevalence of shrubs. The Nevadan is, indeed, largely a forested region; but its open growth is interspersed with vast tracts of chaparral, and altogether fails to produce an effect comparable to the vaster and denser forests of moister climes. Except in the mountains, trees are seldom numerous, and when present form park-like groves rather than true forests. Each region has, too, its meadows, never of large extent, and except in the mountains mostly confined to soils somewhat alkaline.

But throughout the whole territory, shrubs form the common plant-covering of plain and hillside. In the higher mountains impenetrable thickets of *Castanea sempervirens* and *Ceanothus cordulatus* extend for miles. Lower on the Cismontane slope other species of Ceanothus, intermixed with Arctostaphylos, Rhamnus, Ribes, and many other shrubs, cover expanses as wide. To these succeed dense chaparrals of Adenostoma and scrub-oak.

But it is in the deserts that this characteristic is especially developed. Large areas are thickset with opuntias, or with a great variety of other shrubs, daleas, lyciums, ephedras, tetradymias, and many others, whose rigid and thorny growth renders passage painful or impossible. Indeed, in this region, and to a considerable extent in the Cismontane as well, for half the year

the ligneous plants appear to constitute almost the sole vegetation, since the annuals and the aerial parts of most herbaceous plants disappear in the dry season. And even in the rainy months, the superiority of the herbs over the shrubs, in number of species and of individuals, is concealed by their smaller and often insignificant size.

The subjoined table exhibits the vegetative character of the indigenous plants of the different areas. In compiling it I have omitted varieties, doubtful and obscure species, or the few which cannot be satisfactorily credited to any one area. This, it is believed, more fairly represents the prevalent characters of the plant populations, than would the inclusion of every rare and questionable plant.

VEGETATIVE CHARACTERS OF THE FLORA.

Areas	Annuals and Biennials	Herbaceous Perennials	Shrubs	Trees	Total
Desert	167	86	142	9	*404*
Nevadan	79	296	43	19	*437*
Cismontane	359	306	123	25	*813*
TOTAL	*605*	*688*	*308*	*53*	*1,654*

I have classed as trees all those which in southern California commonly attain to fifteen feet (4.5^{m}) in height, and have a tree-like trunk. Of trees 50–100^{ft} (15–30^{m}) high the Cismontane has six, the Nevadan four, and the Desert one; the Nevadan has six which exceed this height, but the other areas none.

RELATIVE PROPORTIONS OF THE DIFFERENT CLASSES OF PLANTS.

Areas	Annuals and Biennials	Herbaceous Perennials	Shrubs	Trees	Total
Desert	0.41	0.21	0.25	0.03	0.24
Nevadan	0.18	0.68	0.10	0.04	0.27
Cismontane	0.44	0.37	0.15	0.03	0.49
Southern California	0.365	0.415	0.186	0.032	

The figures in the first four columns of the above table show the percentages which the number of species in each class of

plants bears to the whole number of species in each area; those in the footing show the proportion of each class in reference to the whole flora of southern California. The right-hand column shows the proportion which the total flora of each area bears to the whole flora.

It appears by these tables that there is a notable difference in the development of the various classes of plants in the several areas. Thus the Desert has the largest proportion of shrubs and the smallest of perennials herbs—a condition which is exactly reversed in the Nevadan area. The Desert and the Cismontane areas have nearly an equal percentage of annual species, and each has more than twice as many as the Nevadan. It also appears that the Cismontane has nearly as many species as both the other areas combined. The percentage of arboreal species is unexpectedly found to be nearly the same in each region, but could the comparison be made between the number of individual trees in each area, the Nevadan would far exceed the others.

The principal cause of these differences is doubtless to be found in the climatic character of the several areas. The short season of winter rainfall in the two Sonoran areas permits the development of annual plants, but is unfavorable to perennial herbs. The cooler climate, and the numerous living streams and springs in the Nevadan area are more favorable to perennials than are the conditions in the other areas. Why the proportion of shrubby species should be so much smaller in the Nevadan than in either of the other areas is less evident, but it is probably due to the occupation of the land by trees, whose shade discourages the multiplication of shrubs. But it is also a fact that the chaparral of this area, while extensive, is composed of fewer species than is the same formation in the other areas.

ADAPTATION OF PLANTS TO CLIMATIC CONDITIONS.

The chief condition of their environment, as I have already stated, to which the plants of southern California have to adapt themselves, those which are paludose or aquatic excepted, is the aridity of the climate, resulting from prevalent high temperature, and a scanty and irregular precipitation. This necessity to some

extent affects even those plants which inhabit the higher mountains, but in a less degree than those which grow at lower altitudes. The mountain plants have a far greater need of protecting themselves against the low temperature of winter. Hence many of them are perennial herbs, which are able to preserve through the winter the vitality of their roots, safely buried in the soil, although the aerial portions perish from the cold. And as the air is here cooler and moister, more plants are found with broad and unprotected leaves than in the other areas.

It is in these other areas that there is the greatest development of the protective adaptations which enable a plant most fully to utilize a scanty supply of water. The methods by which this is effected are three: by habits of growth; by provisions for storing supplies of water and food in times of plenty as reserves for times of need; and by contrivances for diminishing the loss of water through evaporation.

The first of these methods is well exemplified by most of the xerophytic annuals. They spring up at once after light rains, and put forth no more than a leaf or two before proceeding to the production of a flower and a fruit. If moisture now fails, reproduction is assured; should it continue to be supplied, branches are sent out and flowers and seed multiplied. Thus a plant when receiving only a little moisture may fulfil the cycle of existence and provide for the continuance of its species, without attaining an inch of stature; but under more favorable conditions it may attain dimensions of two or three feet.

The xerophytic perennial herbs make their growth in the wet season, and, in most cases, the aerial stems perish at the beginning of summer. Thus they reverse the seasons, remaining dormant in summer to survive the heat, just as in colder climates they remain dormant in winter in order to survive the cold.

The same reversal of the seasons is the habit of many of the deciduous shrubs. They put forth their new foliage in early winter, make their growth during the wet season, and, ripening their fruits in spring, drop their foliage when the droughts of summer come on, remaining leafless and dormant until its con-

clusion. This may be said to be the rule with desert shrubs, and it also prevails to a considerable degree in the Cismontane area.

The storage of supplies at times when they are attainable, so that vitality may be preserved through a season when they cannot be secured, is provided for by a thickening of either the stems or the leaves.

The engorgement of the underground stem or its buds, whereby bulbs and tubers are produced, is comparatively rare among the plants of our region. Among the xerophilous plants of the Desert there are but two bulbs, *Hesperocallis occidentalis* and *Calochortus Kennedyi;* and there are two species of Psoralea and three or four cucurbits which have tuberous roots. A few plants, like the lomatiums, have thickened roots. In the Cismontane area the list of plants of this kind is longer, but not greatly.

The Cactaceae are our only examples of the modification of the above ground stem for storage purposes. During the wet season these stems become plump and full of sap, but at the conclusion of the dry season, they are shrunken and corrugated. This is especially noticeable in the opuntias, but it may be observed also in the appearance of the ribs or the mamillae of the other genera at the different seasons.

Storage in the leaves is exemplified by the agaves, the cotyledons, and the sedums. The leaves of these plants also become more or less shrunken by the end of the dry season.

But much commoner than these modifications are the protective devices by which transpiration is limited. Few are the plants of the deserts which have not acquired one or more adaptations whereby this result is effected. Some, like canotia, the ephedras, the cereuses, and the echinocactuses, are entirely leafless; others, like the opuntias, *Dalea spinosa*, and *Hoffmanseggia microphylla*, have the leaves few, small, and early deciduous. In plants such as these, the modified epidermis is chlorophyllous and performs the office of leaves. In place of the broad thin leaves displayed by the plants of moist climates, these denizens of the deserts have small and thick leaves, often with revolute edges and pinnate divisions. Very commonly the foliage or the whole plant is protected by a coat of hairs, wool, or scales, a var-

nish, or a powder, from the direct contact of the parching air of their arid habitat.

The same modifications are present also in the plants growing in the other areas, but they are not so marked and so prevalent as in the desert vegetation. The ferns may be taken as an example. Only one desert fern (*Notholaena tenera*) is unprotected by a coating of some kind, and although this has small and rigid leaves, its excessive rarity may be taken as an indication of its ill adaptation to its environment. None of the mountain ferns have protective coatings upon their fronds. Eleven of the twenty species belonging to the Cismontane area are destitute of such protective devices, and nine are furnished with them; the former being the species which grow in cool damp situations, and the latter those affecting habitats where the supply of moisture is less abundant or permanent.

STATISTICS OF CLASSIFICATION.

The following table presents a summary of the distribution of the flora into the several taxonomial categories. The fourth column under the head SPECIES shows the percentage of the species in each class to the total number of species. Only naturalized or adventive plants are included as introduced, no notice being taken of escapes or waifs. These exotics constitute but 7 per cent. of the species of the flora, a proportion smaller than is commonly found.

SYNOPTIC TABLE OF CLASSIFICATION.

TAXONOMIAL CATEGORIES.	FAMILIES		GENERA			SPECIES				VARIETIES
	Native	Introduced	Native	Introduced	Total	Native	Introduced	Total	Per cent.	
Gamopetalae	32	1	216	19	235	714	51	765	38	55
Choripetalae	63	1	259	27	280	813	50	863	43	48
Dicotyledones	95	2	475	46	521	1,527	101	1,628	82	103
Monocotyledones	17	..	85	14	99	253	38	291	14	22
Angiospermae	112	2	560	60	620	1,780	139	1,919	97	125
Gymnospermae	2	..	7	..	7	21	...	21	1	1
Spermatophyta	114	2	567	60	627	1,801	139	1,940	98	126
Pteridophyta	7	..	20	..	20	41	...	41	2	2
TOTAL	121	2	587	60	647	1,842	139	1,981		128

Of the families forty-eight are represented by a single genus each, and thirty-eight of these each by a single species. The families which have the most numerous species are shown below, arranged in the sequence of the species:

GENERA AND SPECIES OF THE LARGER FAMILIES.

Families	Genera		Species		Families	Genera		Species	
	Native	Introduced	Native	Introduced		Native	Introduced	Native	Introduced
Compositae.....	99	13	294	25	Labiatae	18	3	44	4
Leguminosae	24	2	149	5	Rosaceae	21	..	42	..
Gramineae.....	37	13	95	30	Chenopodiaceae .	10	3	36	3
Polygonaceae	10	..	85	4	Filices	13	..	30	..
Scrophulariaceae..	14	1	84	1	Ranunculaceae ..	8	..	28	..
Cyperaceae.....	8	..	60	..	Cactaceae.....	4	..	28	..
Cruciferae.....	18	5	51	11	Euphorbiaceae ..	7	1	24	2
Polemoniaceae...	3	..	55	..	Solanaceae	6	..	22	5
Umbelliferae.....	21	6	45	8	Saxifragaceae ...	10	..	25	..
Onograceae	7	..	53	..	Rhamnaceae	4	..	21	..
Hydrophyllaceae..	9	..	52	..					
					TOTAL.....	351	47	1,323	98

From the above table, it appears that these twenty-one families, being but 17 per cent. of the total number of families, include 71 per cent. of all the species which belong in the flora, and that the first ten families include 52 per cent. of the species. Over 16 per cent. of the entire number of species are found in the Compositae, 8 per cent. in the Leguminosae, 6 per cent. in the Gramineae, and 4 per cent. each in Polygonaceae and Scrophulariaceae.

Some of these families, as the Compositae, the Gramineae, and the Cruciferae, owe their prominence to a large number of genera of a few species each; but in others this is due to two or three genera, or even a single genus which has many species. Thus the large development of the genus Phacelia gives importance to Hydrophyllaceae, of Gilia to Polemoniaceae, and of Carex to Cyperaceae; while the rank of the Leguminosae results from the numerous species of Hosackia, Trifolium, Lupinus, and Astragalus, and that of the Polygonaceae from the many species of Eriogonum and Chorizanthe. In the following table the genera which have fifteen or more species are arranged in the order of their number:

GENERA WHICH CONTAIN THE MOST SPECIES.

Genera	Species	Genera	Species
Gilia	52	Trifolium	20
Eriogonum	41	Atriplex	19
Astragalus	35	Chorizanthe	19
Phacelia	30	Mimulus	19
Carex	30	Juncus	18
Lupinus	27	Pentstemon	18
Hosackia	22	Opuntia	16
Krynitzkia	20	Galium	15

The above sixteen genera contain 401 species, or 20 per cent. of all the species of the region. Except a single species of Trifolium, they are all indigenous. It is worthy of notice that these most largely developed genera, with a few exceptions, are distinctively western American.

AFFINITIES OF THE FLORA.

On a previous page I have attempted to indicate the more immediate sources from which our flora has been derived, but it may not be without interest to glance briefly at its relation to the wider problems of plant distribution. For this purpose the families may be divided into three groups: first, those of such equal development in the several zones as be accounted cosmopolitan; next, those having their greatest development in the temperate zone; and, lastly, those whose centers of development are in or near the tropics.

Such an arrangement is shown in the table on the opposite page; Phytolaccaceae and Dipsaceae being omitted, since they are represented only by introduced species. The columns of percentage indicate the proportion of the number of families in each regional division to the whole number of families in each taxonomial group.

It appears from this table that the families, leaving out of consideration the cosmopolitan ones, which, being of general distribution, have no present signification, are about equally divided between the tropical and the extra-tropical groups; a result to be expected from the geographical and climatic position of the region.

REGIONAL AFFINITIES OF THE FAMILIES.

Taxonomial Categories	Cosmopolitan		Extratropical		Tropical and Sub-tropical	
	Families	Per cent.	Families	Per cent.	Families	Per cent.
Gamopetalae	12	37	8	25	12	27
Choripetalae	24	38	21	33	18	29
Dicotyledones	36	38	29	30	30	31
Monocotyledones	12	70	2	11	3	17
Angiospermae	48	43	31	28	33	29
Gymnospermae	..	..	1	50	1	50
Spermatophyta	48	43	32	28	34	29
Pteridophyta	4	57	1	14	2	28
Total	*52*	*43*	*33*	*27*	*36*	*30*

In the next table are exhibited the relations of the native genera and species to the flora of North America. The number of each which extend beyond the North American continent is shown; and those which are confined to it are separated into four geographical subdivisions; namely, those whose range is restricted respectively to southern California, to California, to the region west of the Rocky Mountains, and those which extend further eastward. While the line has been drawn very strictly between plants which are or are not exclusively North American, and as accurately as possible for those confined to western North America, a somewhat laxer rule has been observed for the two smaller subdivisions. These are merely political, and have little phytogeographical significance, and the limits of many of their plants as yet are not known accurately. For these reasons there are included in the number accredited to California, and to southern California, some plants which, while properly belonging to them, extend a little beyond their boundaries.

This table brings out very clearly the distinctively west American character of the flora. Two-thirds of the genera, it is true, extend their range beyond North America; but of the remaining one-third, only 14 per cent. are found east of the Rocky Mountains, while 86 per cent. of this third are confined to the territory west of them, and of these about half

REGIONAL DISTRIBUTION OF GENERA AND SPECIES.

Taxonomic Categories	Genera						Species					
	Endemic					Extra North American	Endemic					Extra North American
	North American	Western N. American	Californian	Southern Californian	Total		North American	Western N. American	Californian	Southern Californian	Total	
Gamopetalae	13	54	16	6	*89*	127	22	250	164	221	*657*	57
Choripetalae	9	42	11	7	*69*	100	55	259	207	187	*708*	105
Dicotyledones	22	96	27	13	*158*	317	77	509	371	408	*1365*	162
Monocotyledones	3	4	3	3	*13*	72	43	88	40	32	*203*	50
Angiospermae	25	100	30	16	*171*	389	120	597	411	440	*1568*	212
Gymnospermae	..	1	..	..	*1*	6	...	13	5	3	*21*	...
Spermatophyta	25	101	30	16	*172*	395	120	610	416	443	*1589*	212
Pteridophyta	..	...	..	..	...	20	4	9	2	6	*21*	20
Total	*25*	*101*	*30*	*16*	*172*	*415*	*124*	*619*	*418*	*449*	*1610*	*232*
Per cent. of native flora	4	17	5	3	30	70	6	33	23	24	87	12

are restricted to California. It will also be noticed that the geographical specialization rapidly increases in passing from the lower to the higher taxonomial groups. Thus all the genera of Pteridophyta extend beyond the North American continent; of the seven genera of Gymnospermae only one is exclusively North American; of the Monocotyledones 15 per cent. are North American, but of the Choripetalae 26 per cent., and 41 per cent. of the Gamopetalae.

Naturally this local differentiation is much more pronounced in the species than in the genera. Less than one-eighth of the indigenous species extend beyond North America. Among the North American species less than 8 per cent. pass beyond the Rocky Mountains; of the species occurring west of that range nearly 60 per cent. are exclusively Californian; of the Californian species over one-half are confined to the southern counties. In the Pteridophyta the species are about equally divided between North American and those of wider distribution; the development of the Gymnospermae is entirely North American; the Monocotyledones are 80 per cent. North American, the Choripetalae 88 per cent., and the Gamopetalae 92 per cent.

COMPARATIVE RICHNESS OF THE FLORA.

A few figures are given below showing the comparative number of species in the southern California and some other floras. The last column indicates the proportion which the species of each flora bears to that of America north of Mexico.

COMPARATIVE TABLE OF FLORAS.

Region	Authority	Date	Area Sq. Miles	Species	Sq. Miles to each Species	Per cent.
N. Am. excl. Mexico	Heller, Cat. N.A. Pl.	1898	.....	14,534	....	..
N. & NW. U. S. Canada, etc.	Britt. & Br., Ill. Fl.	1898	.....	4,162	....	28
Ohio	Kellerman, 4th Cat.	1899	39,964	2,025	19.7	14
Michigan	Beal & Wheeler, Mich. Fl.	1892	56,451	1,746	32.3	12
Montana	Rydberg, Fl. Mont.	1900	145,776	1,676	89.8	11
Alabama	Mohr, Ala. Pl. Life	1901	50,272	2,525	20.0	17
California	Brew. & Wats., Bot. Cal.	1880	156,511	2,956	52.9	20
Southern California	Parish, MS. Cat.	1900	40,889	1,981	20.6	13
Great Britain	London, Cat. 7th Ed.	1877	89,077	1,665	53.5	..

The superiority in number of species of the flora of Ohio, a state having nearly the same area as southern California, is unexpected, in view of the far greater diversity of physical conditions in the latter region. To some extent this is due to an estimate of specific values somewhat more conservative in the enumeration on which the southern California figures are based than obtained in that for Ohio. But mostly it is owing to the fact that the Ohio flora has been long studied, and by numerous able botanists, while our own has had few students, who have worked under disadvantages, and for a relatively short time. Our flora, consequently, is known imperfectly, while that of Ohio has been worked up thoroughly. Additions to it must come mostly from occasional new introductions, or from the segregation of known species. But with us every year's observations of the few resident botanists add a considerable number of species, either new or not previously reported from our region.[29] Other additions are frequently made by those who restudy the accumulated material in the great herbaria. Much territory remains almost wholly unexplored, some of which is certain to

[29] Since my catalogue was completed in 1900 enough additional plants have been reported to make the total number considerably over two thousand.

yield good returns to future explorers. When fully known, the southern California flora will probably contain not less than 2,500 species.

THE CRYPTOGAMIC FLORA.

In this sketch only the Spermatophyta and Pteridophyta have been considered; but below the ferns and their allies lie a series of plants perhaps more numerous than those above them. The relations of these plants, however, to the problems of the life-areas and geographical derivations of a flora is less definite, or at least less understood, than that of the higher groups. Consequently a consideration of them may be omitted in the investigation of these questions, with confidence that a fuller knowledge is not likely to require a reconsideration of the results arrived at.

The information which has been accumulated concerning the representation of these lower plants in southern California is very incomplete. It is almost wholly the result of the labors of two or three students, extended over a short period of time.

The pioneer resident investigator of these, as of the higher plants of the region, was Mr. Daniel Cleveland. In the lower groups he confined his attention to the marine algae of San Diego, and in 1885 published a list of 147 species. Harkness and Moore in their *Catalogue of Pacific coast fungi* (1880) knew of but seven species from the southern counties. More recently Dr. H. E. Hasse has devoted much study to the lichens, the results of which he has made known in several contributions to botanical journals, and by a *Catalogue of the lichens of southern California*, published in 1898. In this are enumerated 304 species, the largest genera being Lecidea, with 65 species, and Lecanora, with 73.

Beyond this almost all that is known of the lower plants of southern California is due to Professor A. J. McClatchie, who in his *Seedless plants of southern California* (1897) laid a broad foundation for future building. A thousand species are catalogued; the lichens are contributed by Dr. Hasse, but the other orders are treated by Professor McClatchie, and are based mostly on his own collections. The Protophyta number 84

species, the Phycophyta 87, the Carpophyta 748, and the Bryophyta 86.

The Musci and Hepaticae appear to be poorly represented in our flora, as might be expected from the arid environment. Of the former Professor McClatchie was able to enumerate but 63, and of the latter but 23, and few additions have since been made to these numbers. This compares poorly with the 312 Musci and the 90 Hepaticae known in the much smaller area of New Jersey.[30]

The lichen flora is more abundant, but is confined to species adapted to arid conditions. Fungi are less abundant than in regions enjoying a moister climate, and this is particularly true of the fleshy fungi. The algal flora, on the contrary, being for the most part unaffected by atmospheric aridity, and enjoying varied environments, is certainly very rich. Of its lower forms the diatoms are abundant and varied, but the desmids, to speak from my own experience, are discouragingly few.

If one descends still lower to those dubious organisms, the Myxomycetes, they also seem to have a very limited representation. For a number of years I have made the collection of the slime-molds a special object, but with very meager results. Only 18 species, representing 12 genera, have been obtained in a condition which permitted determination, a number less than might have been secured in an hour in more favorable climates. I have never found them in abundance, and seldom at all except after long-continued damp and rainy weather.

San Bernardino, Cal.

[30] Britton, N. L., Catalogue of Plants found in New Jersey. 1889.

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

W. F. GANONG.

(*Continued from p. 186.*)

Soil.—Of great importance as an ecological factor is the composition of the soil, physical and chemical. Contrary to the popular belief, the former is at least as important as the latter.

In its physical composition the marsh soil is remarkably homogeneous. Samples taken from the most diverse situations, from the newest layers brought in by the tides, from old long-cropped marsh, from dredgings deep beneath the bogs, are all so alike as to be indistinguishable except for a variation from red to blue in color, and, probably, a somewhat coarser texture of the soil along the banks of the rivers. It is very important to remember, also, that the soil is very deep, even to eighty feet, though usually much less than this. A combination of so homogeneous with so deep a soil must be rare.

In its general characters the dry marsh soil is light brownish red in color, and extremely fine grained in texture. So fine grained is it that only rarely are the individual grains visible to the naked eye. It has no appearance of humus but rather somewhat suggests clay. When the newly deposited layers are exposed to the sun, they harden enough to require a sharp blow to break them, and crack into polygonal areas, concave upward, from a few inches up to two or three feet in diameter, the cracks often being several inches deep and an inch across. When protected from the direct sun, as on the reclaimed marsh, the caking and cracking is much less marked. When again wetted, however, the hard layers melt away into their former state. It sometimes happens on newly plowed ground that a heavy rain

followed by bright sunshine will cause the surface to cake so hard that germinating seeds cannot break through, and much loss is thus caused to crops.

The mechanical nature of the soil will be much more evident from the following mechanical analysis of five selected samples from typical localities, which has been made for me through the kindness of Professor G. E. Stone, of the Massachusetts Agricultural College.

Samples	Water	Organic Matter	Gravel, 2–1 mm Diam.	Coarse Sand, 1–0.5 mm	Medium Sand, 0.5–0.25 mm	Fine Sand, 0.25–0.1 mm	Very Fine Sand, 0.1–0.05 mm	Silt, 0.05–0.01 mm	Fine Silt, 0.01–0.005 mm	Clay, 0.005–0.001 mm	Total
I. Timothy marsh, unplowed for 40 years	2.200	6.505	.025	.275	4.125	9.360	22.185	36.165	10.390	8.585	99.815
II. Low marsh, with poor vegetation	2.600	10.920	.000	.400	.285	1.900	1.300	50.110	17.735	10.530	[24] 95.780
III. Brought in freshly by tide	1.800	6.200	1.125	3.100	2.025	4.225	45.275	14.125	12.400	9.660	99.935
IV. Blue mud from 18 inches under surface	3.160	7.360	.125	.325	2.400	6.210	33.885	20.375	10.865	15.200	99.905
V. From River Habitant, N.S.[23]	3.400	3.200	.125	.260	1.485	4.060	46.010	26.800	8.710	5.825	99.875

These figures confirm the impression made by the appearance of the marsh soils, that they are, as a whole, of unusually fine texture. This becomes yet more evident when they are compared with the results of similar analyses made of various soils elsewhere (as for example the many published in the *Bulletins* of the Division of Soils of the United States Department of Agriculture).[25] Soils of this degree of fineness are far from those adapted to truck and root crops, and are close to those best adapted for grass and grain crops. The fineness of the soil, with its consequent increase of surface for chemical solution, has an important influence upon its fertility, in rendering more easily available such valuable minerals as it possesses. The marsh soils differ, however, from most other fine soils in the smallness of the proportion of clay in comparison with the silt and fine silt. A

[23] A specimen sent me by Professor Shutt.

[24] Obviously a considerable error here; cause unknown. Probably the entire analysis of this sample is untrustworthy.

[25] Or the synoptical article, "Soils in their relation to crop production," by Milton Whitney, in the Year Book of the U. S. Department of Agriculture for 1894.

microscopical examination of the soil shows that it consists of irregular, very angular grains of many different colors and sizes. Very marked and characteristic, in every one of the very many samples of the soil examined, is the occurrence of fragments of sponge spicules, some of the more marked forms of which are shown in *fig. 6*. While these spicules do not form any considerable part of any particular sample, certainly not 1 per cent., nevertheless their aggregate quantity in the enormous deposit of marsh mud is very great, supposing, as the samples indicate, they are distributed everywhere through it. I do not imagine, however, that their presence has any significance whatever in the ecology of the vegetation.[26] Numerous diatoms of several forms are also present in the mud.

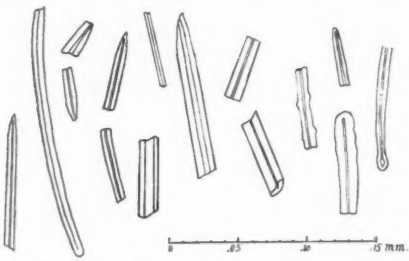

FIG. 6.—Typical forms of sponge spicules from the marsh mud.

The mechanical composition of a soil is important chiefly because of its relation to the supply and circulation of air and water through it. The finer a soil is, other things being equal, the better will it hold water in the hygroscopic state, and hence the better it is for the constancy of water supply to the vegetation. But on the other hand the finer it is the less air will it hold and allow to circulate, and air (*i. e.*, the oxygen) necessary for the respiration of roots is well-nigh as essential a constituent of the soil as water. The soil of the marshes, being much finer than the average, is better than the average for holding and delivering

[26] I think they are without doubt spicules, though they are very fragmentary. They are insoluble in the ordinary acids, and hence are probably siliceous. Very similar forms are figured in the Challenger Report II: *pl. 3, fig. 6*, though I have not seen any branched forms. Two sources of supply are imaginable; living sponges in the Bay and the fossils in the Permo-Carboniferous rocks. But the water must be too muddy for living sponges to flourish, and, moreover, the spicules are very fragmentary, as would be expected if they are ground forcibly out of the rocks, but not if they are floated up from the decay of sponge bodies. Dr. G. F. Matthew tells me fossil sponges are not known from the Permo-Carboniferous rocks.

water, but is worse than the average for aeration. For the latter reason it is adapted only for vegetation with superficial or extremely slender roots, and such the grasses are, while thick-rooted forms, like trees or root crops, needing better aeration, cannot grow, or at least cannot thrive, there.

An extremely important property of soils is their power of circulating water and mineral matters. Every particle of moist soil is surrounded by its film of hygroscopic (and capillary) water holding mineral matters in solution, and these films are in continuity. But the relations of these films to the soil particles and to one another are such that they are, as it were, in a state of unstable equilibrium, so that when water is removed (if not too rapidly) from them at any place, it is restored from neighboring particles, which draw upon others yet more remote, and so on until the equilibrium is restored. And this adjustment is the more perfect the finer the soil. When thus traveling the water carries its dissolved minerals with it. Moreover, owing to the operation of the process of diffusion, the minerals are tending to distribute themselves through the films of water even when these are at rest, from the places where the minerals are more abundant to the places where they are less so. The law of water and mineral movement in soils may be thus expressed: *In a homogeneous soil the water tends to distribute itself evenly throughout the mass, and the soluble minerals tend to distribute themselves evenly throughout the water; a draft at one place upon water and minerals therefore is a draft upon the entire mass if the rate of removal be not more rapid than the equilibrium-restoring power of the soil, which is the higher the finer the soil.* It hence follows that in a homogeneous or nearly homogeneous soil, the plants, if their demands be not greater than the power of the soil to distribute the water, are not dependent for water and minerals simply upon such parts of the soil as can be reached by their roots, but can draw upon the entire mass, the more readily the finer the soil is. Here, I believe, we find the explanation of the lasting quality of the fertility of these marshes when reclaimed; it is due to their depth in combination with their homogeneity, aided by the great water-holding and transferring power given by their fineness of soil. The abundant water

falling upon them as rain, or derived from the melting snows in spring, must saturate the soil to considerable depths, if not to the bottom, thus bringing the water and minerals of upper and lower levels into continuity. Now there is no circulating ground water in the marshes, as the invariable failure of wells dug upon the marshes shows; furthermore they lie below the level of the fresh water of the bogs and mostly below the high-tide level of the sea, and hence there can be no under-marsh drainage, no more indeed than the surface drainage allowed by the shallow ditches or natural runways. This lack of deep drainage has two important consequences; first, there is little or none of that loss of the valuable soluble mineral matters such as is constantly occurring on well-drained upland soils (a fact which alone goes far to explain the lasting fertility), and second, practically the only outlet for the water of the soil is by evaporation from the surface or transpiration through the plants, both of them necessitating an upward movement which tends to bring up the minerals from below. That this effect is actually produced by evaporation is shown by the fact that bald spots even on long-reclaimed, and hence long-drained, marsh always show an efflorescence of salt, and the same is true upon all freshly-exposed surfaces of marsh mud, no matter how long this may have been shut off from the sea. These facts can only be explained by supposing that the salt is brought up constantly from the greater depths. Further, practically the entire vegetation of the marshes consists of the grasses, which both have a comparatively low rate of transpiration themselves, and also protect the ground in an unusual degree from direct evaporation. Hence the upward movement is but slow, and when the warm summer sun promotes transpiration from the plants, the draft made upon the water of the upper soil is not too rapid to allow the latter to recoup itself from the lower layers, and that from a still lower, and so on, to a considerable or even great depth. This upward movement brings with it the minerals, which are not only thus being lifted towards the surface by the ascending water streams, but are constantly diffusing from the lower richer to the upper poorer layers. It can thus come about that the entire depth of the marsh soil is available to the vegeta-

tion above, and it would be only when the minerals from the entire depth are exhausted that the fertility would begin to fail. A corollary of this would be that those marshes whose fertility is most lasting are the deepest, and those soonest exhausted are the shallowest, which certainly agrees in general with the actual facts, as observed and related by those familiar with the marshes.

It is possible that the bogs, which in places underlie the marshes, play some part in this question of water conditions, but we have no facts bearing on this question. As already mentioned, the borings made in the Aulac marsh showed twenty feet of bog lying beneath the eighty feet of marsh mud. Mr. Chalmers is of the opinion that bogs extend practically everywhere beneath the marsh, but I do not think this is probable. If the mode of formation of the marshes in the earlier stages, given earlier in this paper, is correct, it is plain that the marsh could have formed without covering any bog except that which may have existed in the fresh-water lake in this basin before marsh-formation began. Bogs, however, could be buried under mud through natural changes in the courses of the rivers, and they are now often buried in the operations of bog-reclamation. Such places are said to be better drained and to bear larger crops than similar marsh not underlaid by bog.

There are other physical properties of soil of much importance to the vegetation occupying it, such as its permeability to air, its power of absorbing and retaining heat, etc., but for the marsh mud no data at all are available upon these properties.

We pass next to consider the chemical composition of the marsh soil, upon which some satisfactory data are available. Five samples carefully collected by myself in 1898 from different typical situations on the marshes, and of four of which the mechanical analyses have been given on an earlier page (281), have been carefully analyzed for me by the courtesy of Professor Frank T. Shutt, chief chemist at the Chemical Laboratory of the Dominion Experimental Farm at Ottawa, with the following results.[27] To these are added an analysis made at the same lab-

[27] A full discussion of these analyses by Professor Shutt may be found in the Report for 1901, cited in the Bibliography.

oratory, of a similar marsh soil from Cornwallis Valley, Nova Scotia:

Samples	Organic and Volatile Matter	Clay and Sand	Oxid of Iron and Alumina	Lime	Magnesia	Potash	Phosphoric Acid	Soluble Silica
I. Timothy marsh, unplowed for 40 years	6.54	75.29	14.72	.239	.513	.817	.136	.091
II. Low marsh, with poor vegetation	10.60	73.18	12.64	.234	.397	.852	.124	.059
III. Brought in fresh by the tide	6.02	75.83	13.79	.652	.283	.902	.146	.063
IV. Blue mud from 18 in under surface	6.77	76.01	14.01	.409	.183	.996	.094	.056
V. From 30 in below surface under canal above Point de Bute	3.10	84.48	9.87	.288	.154	.646	.110	0.63
VI. From River Habitant, N. S	4.14	75.59	11.71	1.40	.48	.25	.15	.....

Samples	Carbonic Acid, &c., Undetermined	Total	Nitrogen	Available.[28]			Reaction	Common Salt
				Potash	Phosphoric Acid	Lime		
I. Timothy marsh, unplowed for 40 years	1.654	100.0	.182	.0088	.026	.0626	Acid.	.037
II. Low marsh, with poor vegetation	1.914	100.0	.338	.034	.016	.0449	Acid.	1.048
III. Brought in fresh by the tide	2.314	100.0	.122	.0748	.0466	.397	(*)	4.16
IV. Blue mud from 18 in under surface	1.472	100.0	.106	.0073	.0436	.0792	Acid.	.939
V. From 30 in below surface under canal above Point de Bute	1.289	100.0	.062	.030	.0354	.108	Acid.	.217
VI. From River Habitant, N. S	.....	.....	.128	.06	.05	.....	.....	.86

An abstract of the remarks made upon the samples by the analyst is as follows:

No. I. As to humus (organic matter) nitrogen and lime, about as in soils of average fertility; potash in this as well as the others, much higher than in

[28] The "available" quantities are attained by the Dyer citric acid method. Compare the report by Shutt, just mentioned.

* Neutral or slightly alkaline.

most virgin soils, existing probably as double silicates likely to be gradually liberated in available form by good culture and favorable climatic conditions; phosphoric acid somewhat lower than in virgin soils of average fertility, but a large amount of it is in available form; oxide of iron large in amount, a favorable feature for fertility under proper cultivation; immediately available potash not abundant in this sample, probably because removed for so many years by the hay crop, but available phosphoric acid fairly abundant.

No. II. Shows nearly double the organic matter and nitrogen of no. I; also much richer in potash, total and available, but has less phosphoric acid. If properly drained should give results as good as no. I.

No. III. Of special interest as showing the composition of the original soil as brought in by the tide. Shows nearly three times the lime of nos. I and II, no doubt because so much lime has been removed from the former with the crops.

No. IV. Not positively deficient in substances needful for fertility but mechanically unfavorable. (Compare remarks on these blue soils on the next page.)

No. V. Not appreciably different from the others except in its smaller proportion of nitrogen and humus, which is explained by its deeper position.

No. VI. Not richer in mineral matters than many soils of average productiveness. But a discrimination between the total amounts of the important substances, and the amounts immediately available, shows a remarkably large proportion of the latter, as compared with other fertile soils, and probably in this feature consists a large part of its richness.

With these it is of interest to compare an earlier, and apparently careful, analysis given by Dawson, in his *Acadian Geology* (third edition p. 23) of a "Red soil from Truro, recently deposited":

Moisture	.5	Organic matter	1.5
Soluble in water		Carbonate of lime	3.60
Chlorine (as common salt)	.095	Oxide of iron	2.74
Soda (as common salt)	.115	Alumina	1.20
Potash	.013	Magnesia	.11
Sulphuric acid (as gypsum)	.073	Soda and potash	.8
Lime (as gypsum)	.061	Phosphoric acid	.09
Alumina	.005	Siliceous sand (very fine)	88.00
Magnesia	.004		

Trueman gives some analyses, very imperfect, however, of these soils in his paper (page 104),[29] and some others are found

[29] Eaton, in his most excellent account of the marshes, points out what he thinks a chemical difference between the marshes of Minas Basin and those of Chignecto Bay in that the former contain larger quantities of salts of potash, lime and alumina.

in the various reports of the chemist of the Experimental Farm, cited in the Bibliography.

The marsh soil, however, is not always red and rich, but it is in places blue and barren. This blue soil occurs in low badly drained places, is but a few inches deep, and is underlaid by red soil, which occurs everywhere in a layer under the bogs. Bands of it appear occasionally on river banks in the rich well-drained marsh; but, as already pointed out, this is without doubt due to the wandering of the rivers, which, in changing their courses, cut into spots previously back from their courses and badly drained. The blue soil seems, however, at times to underlie the "sedge-bogs" along the rivers. A full account of the formation of this blue soil is given by Dawson in his *Acadian Geology* (p. 24 of the third edition) as follows:

> The chemical composition of this singular soil, so unlike the red mud from which it is produced, involves some changes which are of interest both in agriculture and geology. The red marsh derives its color from the peroxide of iron. In the gray or blue marsh the iron exists in the form of a sulphuret, as may easily be proved by exposing a piece of it to a red heat, when a strong sulphurous odor is exhaled, and the red color is restored. The change is produced by the action of the animal and vegetable matters present in the mud. These in their decay have a strong affinity for oxygen, by virtue of which they decompose the sulphuric acid present in the sea-water in the forms of sulphate of magnesia and sulphate of lime. The sulphur thus liberated enters into combination with hydrogen obtained from the organic matter or from water, and the product is sulphuretted hydrogen, the gas which gives to the mud its unpleasant smell. This gas dissolved in the water which permeates the mud, enters into combination with the oxide of iron, producing a sulphuret of iron, which with the remains of the organic matter, serves to color the marsh blue or gray. The sulphuret of iron remains unchanged while submerged or water soaked, but when exposed to the atmosphere, the oxygen of the air acts upon it, and it passes into sulphate of iron or green vitriol—a substance poisonous to most cultivated crops, and which when dried or exposed to the action of alkaline substances deposits the hydrated brown oxide of iron. Hence the bad effects of disturbing blue

These substances he supposes to be derived from the trap rocks at the entrance to Minas Basin, which rocks are absent on the Chignecto Branch. Hence he says, the Minas marshes have shown no signs of exhaustion, while the Chignecto marshes have. Comparative analyses of samples from both sets of marshes as far as available do not sustain this contention, nor, indeed, as far as I can learn, is he correct in his estimate of the relative lastingness of the fertility of the two sets of marshes.

marsh, and hence also the rusty color of the water flowing from it. The remedies for this condition of the soil are draining and liming. Draining admits air and removes the saline water; lime decomposes the sulphate of iron and produces sulphate of lime and oxide of iron, both of which are useful substances to the farmer.* [*Since the publication of the first edition of this work, the blue marsh of Nova Scotia has been extensively improved by this process.]

Grouping together the facts as to chemical composition, it is plain that the marsh soil as a whole is rather uniform in composition; that it is chiefly composed of fine siliceous sand with an average of about 10 per cent. of clay; that it naturally contains but little organic matter, which only develops sparingly with the denser vegetation of the reclaimed marsh; that it contains percentages of potash, lime, phosphoric acid, and nitrogen, approximating those of good virgin soils elsewhere, but with an unusually large amount of those substances in an immediately available form; and that the amount of common salt varies with the degree of reclamation. The above facts amply explain the fertility of the marshes, more especially when it is remembered that the chief, almost the sole, crops are grasses, which are not very trying to the soil, and to which the above combination of substances and conditions is particularly favorable. The lasting quality of the marshes is not thus explained, but that, as I have earlier shown, is without much doubt due to their depth and homogeneity, whereby the entire mass to the bottom is made available to the vegetation. These two sets of factors together, I believe, amply explain the agricultural value of the marshes.[30] The composition of the marsh soil as a whole is doubtless very similar to that of the red sandstones of this region (with, perhaps, some salt added from sea-water), which constitute some of the richest upland soils in the provinces. The resemblance is

[30] There is in the marsh country a popular misunderstanding of this subject. It is customary for the residents to say that the analyses of the soil which have been made reveal only clay and sand, with nothing to explain its fertility, which they think must therefore be due to some cause still unknown. No doubt the smallness of the percentages of potash, lime, nitrogen, etc., mislead those unacquainted with the chemistry of soils. In fact the richest soils contain as a rule less than one per cent. of each of those important substances, and quantities much over one per cent., so far from making the soil richer, actually injure it, for the roots of plants are unable to absorb any but very weak solutions of mineral substances.

of course genetic, for the marshes are such soils pulverized and leveled by the sea.

The analyses show further the comparative poverty of the marsh soil in lime, certainly the greatest defect of the marshes, and this substance is the first which has to be added to degenerating marsh. This fact is of much importance ecologically, for to the absence of lime is due the possibility of the formation of sphagnum bogs so extensively developed with the marshes, the sphagnum not growing where lime occurs. The neighboring upland, composed of Carboniferous sandstones, also is free from lime.

The form of occurrence of nitrogen in a soil is very important to its fertility, and as to this the analyses give us no information. The amount of available nitrogen in a soil is closely correlated with the presence of bacteria, and here also, for the marsh soil, we have no data. The bacterial content is not likely to be large, however, since there is so little humus, on which they are dependent.

We must next consider a special phase of soil composition very important to our present subject, namely, the presence in it of common salt (sodium chlorid) derived from the sea water. In minute quantities (small fractions of 1 per cent.) salt in the soil, since it has no part in plant nutrition, does not appreciably affect vegetation as a whole, though it may influence individual forms; but when the percentage rises toward 1 per cent., its presence begins to be of consequence, while above 1 per cent. and upwards it produces profound effects upon the form and distribution of the vegetation. It acts both chemically and physically; chemically in that the plant cannot help absorbing it with the water and it affects injuriously some of the vital processes,[31] and physically because roots are unable to absorb water osmotically (their only method) where more than a very small amount of salt is present. With most roots water cannot be absorbed at all if it contain as much as 1 per cent. of salt and none can absorb it from a solution much, if any, stronger than 3 per cent. As to the amount of salt contained in the marsh soil,

[31] It can of course do this without acting positively as a poison; to what extent the salt is positively poisonous is still uncertain, though the studies of Loeb, True, and others seem to show that in some cases it is so.

that of course varies greatly, as the table on page 286 shows, with the degree of reclamation, etc., and it is this variation which is responsible for the profound differences in the vegetation of the different parts of the marshes. The water of the sea, which has everywhere laid down these marshes, and countless times has overflowed every part of them, must be very nearly the pure salt water of an open sea coast, that is, it must contain near 3 per cent. of salt. This is not only indicated by my tests (unhappily few and crude) of the density of selected samples (tested with an hydrometer), but also by the fact that the fresh-water streams of this region are comparatively insignificant in volume, and the swirling tides mix the fresh water thoroughly with the salt, preventing it from lying on the surface. Not only has every part of the marshes been as salt, or nearly, as the sea, but in places they are much salter, for, owing to the building up of the banks next the sea, there are many pools formed on the marshes into which the highest tides can run, but from which the water does not escape, remaining to evaporate and leave its salt. In many places on the unreclaimed marsh, especially between rivers, such pools exist, much too salt for any vegetation except a few simple algae; and it is quite probable that it is such former pools on the now reclaimed marsh which form the poor or bald places, later to be mentioned, so difficult fully to reclaim. On the other hand, although on the reclaimed marsh no new salt is being added, and the salt already there is being steadily removed by rains, by drainage, and with the crops, it appears never to be entirely removed, no doubt because it is constantly being renewed by diffusion, aided by evaporation, from greater depths. This is shown both by the analyses on page 287 where even the long reclaimed English hay marsh is shown to contain an appreciable amount, and other places a considerable amount, but also by the fact, well known in the marsh country, that an efflorescence of salt ("salt enough to taste," the residents say) is to be seen at times, after dry weather, on the surface of even the oldest reclaimed marsh. Further, the mud brought up from beneath the fresh-water bogs by the canal dredges, shows, as I have myself seen, a marked efflorescence of salt in drying. The

data as to the amount of salt in the reclaimed marsh are unfortunately scanty, but it seems safe to say that it must be on the best marsh much less than half of 1 per cent. and it grades from that upward in all degrees to the wild marsh, which may contain up to 4 per cent., or, in special places, considerably more. It is the presence of this salt even in the reclaimed marsh, which, more than any other cause, keeps the marshes treeless; the salt prevents that ready osmotic absorption essential to large vegetation.

The distribution of salt in the reclaimed marsh is not uniform, however, for places occur in which the vegetation exhibits markedly, or even extremely, a salt-marsh character. These places are of three sorts. First, there occur certain "bald spots," of no apparent determinants, on which only scanty salt-marsh plants grow, or, in certain cases, none at all. These may be remnants of ancient pools mentioned in the preceding paragraph. They can be rendered productive, however, which is effected by covering them with brush (branches of spruce, etc.), straw, loose boards, or other convenient material for two or three years, after which they bear the ordinary grasses of the surrounding marsh. Of course this comes about through the fact that the rain washes out the salt from this soil, and the ground being protected from evaporation, no new supply is brought to the surface by the rising water. Second, on marsh that is improperly drained, there are occasional low spots into which the rain settles from the neighboring higher parts, of course carrying with it some dissolved salt which is concentrated as the water evaporates, thus allowing only a salt vegetation. Third, the farm roads across the marshes, though little used, are always marked by lines of salt plants, often indeed in most striking contrast to the rich hay grasses on each side of them. The presence of the greater quantity of salt along the roads is due, I believe, to a cooperation of two causes; first, the travel over such roads tends to keep down the grasses and to leave the ground somewhat bare, so that evaporation from these places is much more rapid than from the neighboring densely grass-clad ground and the salt must therefore be drawn to the surface more abundantly

there than elsewhere; second, the travel tends somewhat to compact the soil on the roads, and evaporation is more rapid, other things being equal, from a compact than from a loose surface of a homogeneous soil, hence contributing to bring up the salt. In places, too, the roads are lower than the neighboring surface, so that water would tend to drain into them with its salt, which would be concentrated by evaporation; but this is not the main cause of the presence of the salt plants there, for they occur on high as well as low places. On the other hand, the places on the marshes which seem to become most free from salt are three. First, there are the dikes and the ridges thrown up in digging the ditches; the ditch-ridges in particular become so free of salt as to permit not only upland salt-shy weeds to grow but even the still more salt-shy bushes, such as alders, roses, etc. Their freshness is due, no doubt, in large part to the perfection of their drainage, but it is more the result, I believe, of the lack of homogeneous continuity between the somewhat loosely heaped ridge and the compact marsh soil, whereby the continuity of the hygroscopic soil water is interrupted and hence the upward movement by evaporation largely diminished. The comparative looseness and roughness of the ditch-ridges, also, like cultivation in a garden, lessens evaporation, which with the preceding factor permits the removal of salt here to be more rapid than its renewal. Second, there are the spots on good high marsh where hay-ricks have stood, on which a luxuriant weed-vegetation grows up. Plainly the causes are here as above indicated for the bald spots; the ricks preventing evaporation, there is no rise of salt to these places, but rather, by the movement of the water falling here as rain, a washing away of the salt to neighboring places. Much the same effect is produced by the shade of the barns. Third, there are occasional, though rare, spots on the high marsh, not in any way shielded from evaporation, on which weeds, and even small bushes, and in one case a small birch tree, stand. These places appear to me to be always on old and shallow marsh, and represent, I think, spots from which the salt has been in course of time largely removed by drainage and the crops.

Animals.—Animals through divers of their manifold activities may play a large part in phytoecology, but in the case of these marshes their influence appears with but one important exception to be insignificant. That exception is the animal commonly called man, who has developed the habit of providing himself with food by cultivation (in which respect he is by no means unique, but was long anticipated by the fungus-raising ants and others), and to this end has performed two operations of much importance in the ecology of the marshes: first, he has shut out the sea from great areas, thus allowing their conversion from a salt to a nearly saltless soil with the enormous change in their vegetation thus implied; and second, he has brought from other countries certain special kinds of plants which he has let run wild on these marshes. The latter point needs especial emphasis, since it is so liable to be misunderstood. A stranger, even a botanist, visiting for the first time the reclaimed marshes, and looking upon their extensive fields of rich grasses, is likely to think that they are kept in that condition only by careful sowing and frequent renewal, in the absence of which they would soon be replaced by other vegetation. This is what would soon happen on good upland hay fields, for instance, which soon revert to patches of wild weeds and later to forest. But such I believe would be not at all the fate of these marshes. It is of course true that if they were totally neglected by man, the drains would soon fill up, and the dikes would be broken down and washed away, after which the whole region would return to the condition of wild salt marsh. But if, in some way the dikes and drains could be made perpetual, I believe that the present English hay grasses could maintain themselves indefinitely, or at least as long as the fertility of the marshes lasts, without care from man, and they would not as a whole be replaced by any other vegetation. In other words, the English hay grasses brought in by man appear to be the very vegetation best adapted to the conditions prevailing on the reclaimed marsh, and no other, certainly no native plants, could drive them out. Many facts sustain this rather remarkable conclusion, of which the most important is this, universally stated

by those who work with the marshes, that when the marsh is diked and drained, a natural succession of plants follows the freshening of the marsh soil, ending with the English hay grasses, which come in of themselves without any artificial seeding or other aid whatever. They could not do this if there were other plants in the vicinity better adapted to the new conditions. Moreover, having once established themselves in this way, they maintain themselves indefinitely without cultivation. It is true, as already mentioned, that at regular intervals the marsh is generally plowed, but this is by no means to aid these grasses in their competition with other plants, but is mainly to renew the stock on special places to keep it up to the very highest condition of productive vigor. The case of marsh not plowed for over forty years, and still bearing the English grasses with apparently undiminished vigor, shows that the plowing is not essential. Man, therefore, has both created a new field by diking the marshes, and has also brought in a vegetation better fitted than any native vegetation for that field. Later the question of why this introduced vegetation is better than any native kind for this situation will be discussed.

It is an interesting question as to what appearance these great expanses of marsh would present today had man never reclaimed them. We cannot doubt that they would be salt marsh like the still unreclaimed pieces. The fact that the marshes are still sinking, or at least are not rising, would prevent any natural recovery and building up by the action of large vegetation, such as is occurring at the mouth of the Rhone, as described by Flahault and Combres, though were the region rising such a result would probably occur.

As to other animals on the marshes, insects seem fairly abundant, and of course play their part in the pollination of the plants which have showy flowers, but as the greater part of the vegetation is anemophilous, or wind-pollinated, their influence is not ecologically important. Birds occur as in upland meadows. Mosquitoes are abundant and voracious. Various fishes occur in the ditches and canals, and frogs and muskrats are abundant in the fresh-water streams. None of these appears to have any

determinable influence upon the vegetation. An animal important in the economy of soils, namely the common earthworm, is said by the residents not to occur upon the marshes. I have seen what appeared to be their castings, but have been told by an intelligent observing farmer that these are in reality made by some burrowing insect.

Geography of the basin.—To the ecological factors already considered there must be added another of a different sort, namely, the geography of the basin itself. We have already considered one phase of this subject, for upon the latitude, elevation, proximity to the sea, to cold or warm ocean or air currents, depend some of the ecological factors previously discussed. But in addition there are two other important phases of the subject. First, there is the geographical position of the region relative to the great floristic divisions of the earth's surface, upon which depends its flora (as distinct from its vegetation, which is determined by the preceding), and the flora determines the materials upon which the particular ecological factors of the region are to work. In this case we are dealing with a portion of the region covered by the temperate North American flora, with all the peculiarities of species, genera, and families thereto belonging. Second, there is the degree of isolation of the basin from the neighboring regions. Isolation may be brought about principally by the presence of natural barriers, mountain ranges, wide arms of the sea or desert, or even to some extent by great size. Isolation is ecologically important, for upon it depends the possibility of the rapid development of indigenous and exceptionally adapted forms. It produces this result both by preventing the dilution of new adaptive characters through crossing with immigrants from without, and also by preserving undiluted those characters which may be developed independently of adaptation. Regarding now the marsh country from this point of view, we see at once that it is entirely without natural barriers of any kind, and lies open in every direction to immigration from sea-shore, field, and forest; while it is so small in extent (nowhere exceeding four or five miles in diameter), that the natural modes of locomotion of most of the plants

round about can carry them readily to every part of it. Under these circumstances there is not, nor can there be in the marsh-land, any development of extreme adaptations, much less of new types. What happens is this—the ecological conditions here prevailing select from the great mass of forms which are constantly brought to them by natural modes of dissemination, the particular forms that happen to be best adapted to those conditions, rejecting, by suppression, all others. Further, as I believe, having selected the best adapted, their adaptations are in such a basin improved and intensified, so that these forms are being distributed from the basin in a better adapted condition than they enter it. Probably it is a general rule that the larger and more isolated the basin the more the tendency to develop peculiar types; the smaller and less isolated the basin, the more is it a case of selection of forms brought constantly into it and their improvement, such small basins serving as centers of distribution of better adapted forms. The ecological interest of these marshes lies, not in any peculiar adaptations they show, but in the perfection with which they exhibit many phenomena of adaptation.

Summary of the ecological factors: the responsive type of vegetation.

The various physical features we have just considered constitute a set of conditions to which the vegetation must conform. Since no development of a special vegetation to fit them is possible, we ask what forms of the plants of this region do come nearest to fitting those conditions and hence actually occur there. So far as the general climatic conditions are concerned, the responsive type for this region, as I have elsewhere shown,[32] is a mixed mesophytic forest, such as actually occurs on the neighboring uplands. But on the marshes there comes in another factor which is of the first importance and is prepotent or determinative, namely, the peculiar soil. This requires that the marsh vegetation shall be such as has a superficial or very slender root

[32] The vegetation of New Brunswick as a whole I have considered in Bull. Nat. Hist. Soc. New Bruns. 5: 52. 1903.

system, thrives in a siliceous and somewhat salt soil, needs a constant rather than a great water supply, can spread a mesophytic foliage to the summer sun and retreat to a winter xerophytic condition, can endure exposure to unshaded sun and strong winds and not spread too great a surface to their transpiring influence, and can use the wind in dissemination and cross-pollination. No one form of vegetation can be found to fit best all these conditions, but any ecologist can tell at once what type comes the nearest to fitting them in the aggregate; it is the grasses and grass-like plants. This is why the vegetation of the marshes is so overwhelmingly of that kind.

The plants of the marshes.

We turn now to consider in some detail the vegetation of the marshland, and naturally ask first what kinds of plants live there. No attempt has yet been made to prepare a flora of the marshes, and such scanty lists of species as exist have already been mentioned (page 162). From the point of view of ecological plant geography, however, their floristic completeness is of slight importance, since the character of the vegetation is determined by only a few prominent forms, and all of those rarer and less conspicuous species, naturally of such interest and importance to the floristic student, might be wanting without affecting the characteristics of the vegetation as a whole. Further, the species, as such, are not of special concern ecologically. What is here important is this, the species as an aggregation of adaptations, that is, as a vegetation- (or life-, or biologic) form, for these vegetation-forms are the unit of the ecologist as the species are of the systematist. In a general way species and vegetation-forms may not be coincident. Thus the same vegetation-form may be developed under similar ecological conditions from very different and widely separate species, as witness Agave-Aloe, Calluna-Erica, and Cereus-Euphorbia (some), but this does not hold true in minutiae, and such forms as those above mentioned, while alike in most characters, differ in many particulars. This is of course because plants are not indefinitely plastic to environmental influences, but are limited much

in adaptation by their heredity, and a different heredity does not permit two distantly related plants to be brought into ecological identity at all points. Hence for purposes of detailed ecological study, and as well because of practical convenience, species and vegetation-forms are coincident, though the point of view from which they are regarded by systematist and ecologist is different. This treatment of the two as coincident is the more necessary at present because of the undifferentiated state of knowledge and terminology of the vegetation-forms,[33] a subject greatly in need of systematic study and formulation. In the following pages I have attempted to indicate a few of the characteristics of the principal species[34] treated as vegetation-forms, especially in the case of *Spartina stricta*, and the ill-success of the attempt is at least in part due to the imperfections in our knowledge of this subject, a matter on which further comment will be found later in this paper. Much work has of course been done upon the anatomy of all of these plants, and Kearney has summarized it in some of the forms, but I have not attempted to treat this phase of the subject.

The vegetation of the marshland.

The vegetation-forms of any region taken together constitute its vegetation. The units, however, are by no means mixed at random to form the mass, but are grouped differentially in

[33] This term, used by Pound and Clements, while better than the "life-forms" of Smith and the "biologic forms" of the translation of Flahault, is far from satisfactory, since the word *form* is somewhat ambiguous and the phrase does not convey an idea of the real significance of the vegetation-form either as a unit of the vegetation, or as a resultant of adaptations. A proper terminology of vegetation-forms (a beginning in which has been made by Pound and Clements) is especially needed in order to allow the forms of different countries to be compared, which they cannot be if simply named for their species.

[34] All of the species listed in the following pages, unless otherwise mentioned, have been confirmed or determined by Mr. Walter Deane, of Cambridge, Mass., with the exception of a few of the grasses which have been named by Mr. F. Lamson Scribner, of Washington, and to both of these botanists I must express my sincere thanks for their kind aid. The English names given are in all cases those by which the plants are locally known in the marsh country. The nomenclature is that of the sixth edition of Gray's Manual, to which in brackets are added the synonyms made use of in Britton's Manual.

accordance with definite factors. This grouping, and its causes, so far as known, we have now to consider for the marshland.

The vegetation of any region develops, in response to the great primary ecological factors of temperature and precipitation, a characteristic climatic type, which prevails wherever no limiting factor becomes prepotent. For the region in which the marshland lies, this type is a mixed mesophytic forest, as shown upon the neighboring uplands. Further, according to Cowles' theory, which seems to me in general well-grounded, all the vegetation of a region is tending to approach this type, because the vegetation is very closely correlated with physiographic factors, and physiographically any region is in general tending to approach a base-level uniformity. This tendency involves the elimination of prepotent secondary factors, and hence the approach of the vegetation to the climatic type. The marshes appear to offer an exception to this rule, an exception more seeming than real, as will later be noticed.

On the marshland, however, certain limiting factors do become prepotent, determining marked deviations from the climatic type and hence divisions of the vegetation as a whole, namely, *the presence of abundant salt in the soil*, determining a HALOPHYTIC DIVISION, *an accumulation of fresh water* determining a HYDROPHYTIC DIVISION, and *the influence of man*, which removes large sections from the halophytic to the MESOPHYTIC DIVISION, or rather to a special section of it which may be called the *culture section*. The fourth of the principal vegetation divisions, the xerophytic, is not represented in the marshland. These divisions, however, are by no means of homogeneous appearance, but their vegetation falls into distinct groups of plants, the prominent forms of which have the same general aspect and adaptations, and occupy and are correlated with distinct physiographic positions. Such groups are called *formations*. They usually form distinct features of the landscape, and are known by distinctive local names expressing the physical habitat, such as bog, marsh, etc. But the formations, more closely observed, do not show an even mixture of plants, for these are grouped or segregated into definite assemblages, dependent in some part

upon degrees of the physical factors determining the formations, though in larger part upon a quite different principle, namely, the ecological interrelationships of the plants to one another, particularly with reference to the ability of different forms to occupy the same ground at the same time without serious interference and perhaps with positive benefit to one another. Such groups are called appropriately *associations*, and they often are recognized and named locally by the prominent forms, such as oak-forest, broadleaf marsh, etc. Formations and associations are thus both distinct ideas and distinct groups, the former having the physical or physiographic idea prominent, and the latter the idea of ecological interrelationships of the plants, involving their competition and cooperation. Of course the two merge into each other, and often coincide, and by many students they are treated as one. Their delimitation, while often easy, is sometimes very difficult. As in all such cases they can be studied and described only by the selection of typical examples, all intermediate forms being described in terms of the typical. The associations are made up of the *vegetation-forms*, the ecological units, best treated for the present, as above explained, as coincident with species. These vegetation-forms constitute the *members* of the association, but of varying degrees of importance. Some are evidently far in the lead in size, numbers and importance — they are dominant; others are close to these and struggling for the leadership — they are secondary; others are much less conspicuous, but manage to maintain a position among the preceding in spots not occupied by them — they are subordinate. Then in addition to the members may be recognized the frequent visitors from neighboring associations, and various strangers or stragglers from more distant positions. But a satisfactory terminology of the degrees of membership must await an understanding of the real nature of their interrelationship, a knowledge which we do not yet possess.[35]

[35] The distinction here drawn between formations and associations will not be admitted as valid by all, at least to the degree here held, but I believe it represents a real fact in nature and will stand. There is moreover an increasing tendency to recognize the distinction as well as to use this terminology. It is used by Kearney, by Lloyd and Tracy, and by Harshberger (though he calls the association a society).

The various associations of the marshland, named according to their dominant forms, together with their formations to which they belong, are shown by the following synopsis.

Clements lays much stress upon the formation, but gives the association a subordinate place, designating it as "patch." Cowles recognizes formations (under the name of society) but gives no separate importance to the association. Smith recognizes the formation under the name of association, but combines features of both. Warming recognizes the formation (calling it *Verein*), but hardly the association as a distinct group; and the usage is similar in Schimper and Drude. In all these cases, where the one is distinguished and not the other, the facts are of course recognized, though the two groups of ideas are consolidated as it were into one. In such cases the idea of the association is often brought out as a "facies," etc. The complicated history of the use of these terms may be traced in the works of Smith and Flahault cited in the bibliography. The words formation and association as here used seem to me good terms, and should be adopted. The word society could better be restricted to those ecological groups of another kind, such as epiphytes, parasites, etc. Clements has recently made a carefully considered proposal for nomenclature of formations, and I have given some of his names later in this paper. The associations are best distinguished by their dominant forms with the termination *etum*.

[*To be continued.*]

BRIEFER ARTICLES.

A NEW SPECIES OF GEASTER.

(WITH TWO FIGURES)

In February 1903, I received through Dr. W. C. Coker, of the University of North Carolina, Chapel Hill, N. C., a pretty little Geaster, growing on the bark of moss-covered living trunks of trees in the woods. The first specimens which I received were collected by one of the students at the University, Mr. C. A. Shore, and afterwards very abundant material was collected both by Mr. Shore and Dr. Coker.

The species is quite remarkable in several respects. In the first place, its habitat on bark of living trees is unusual, for while now and then a species normally growing on the ground or on dead logs may be found around the bases of trees on the dead bark among moss, the distinctive habit of this species is upon the dead bark of living trees some distance from the ground. In this respect it is similar to the puff ball, *Lycoperdon leprosum* B. & R.[1] In fact, it sometimes grows intermingled with specimens of *Lycoperdon leprosum* on the same tree, so it may occur as an associate, or as the only puff ball on the tree. Thus far it has always been found among moss, and it will be interesting to know if there is any mutualism between the moss and its associate Geaster, of such a nature that the Geaster is dependent upon the moss, or whether the conditions of moisture, etc., which are favorable for the growth of the Geaster in all cases observed, bring about also the development of the moss, so that the association of the two is merely accidental.

It is also remarkable in another respect, that it belongs to the fornicate section of the genus, a section which contains but a very few species in comparison with the large number known. The third unusual character of the species is that the spores are smooth, not echinulate or tuberculate, as in other species, although the spores are more or less irregular, with three to four slight angles in side view. Usually these angles are not prominent, and under the low power of the microscope the spores appear to be perfectly globose. At first

[1] *Lycoperdon leprosum* B. & R., Rav. Fung. Am. Ex. no. 14. See also Pk. Mon. Lycop. 29.

I thought the spores were white, and they are colorless in specimens which are not very mature, but when the plant is quite mature, the inner peridium well opened and more or less collapsed, the spores mostly have a pale yellowish-brown color. The plant is attached to the moss and the bark by numerous threads, which radiate irregularly from the outer cup-shaped layer of the outer peridium, and the mycelium extends also into the dead bark, penetrating more clearly through the lines of cleavage in the bark, both radial and tangential.

FIG. 1.—*Geaster leptospermus.* Smaller plants, upper right hand corner, natural size. Others × 2.5, the one at the left collapsed and broken away from cuplike base, which is also collapsed, but is shown as a well formed and distinct layer. Plant at extreme right in early stage of dehiscence; outer peridium split into 4 rays.

In some cases delicate rhizomorphic strands are developed quite abundantly in the tangential cleavage planes. The plants are whitish, but when mature pale gray in color. They are oval to globose, 3–4.5 mm in diameter. Before the dehiscence of the outer peridium takes place, the plants are inconspicuous and appear as minute rounded bodies, or minute convex whitish surfaces in the moss. But after dehiscence takes place the fornicate character of the plant lifts the inner peridium so far above the moss that it is quite conspicuous, except for its minute size. When dehiscence of the outer peridium first takes place it splits radially into three or four rays, showing the white granular surface of the inner peridium, with its well defined mouth, which is radiately silky, but not sulcate nor striate. The inner face of the outer peridium is also seen to be granular. As the plant expands more the inner layer of the outer peridium separates from the outer

layer and is everted, the points of the rays remaining attached to the points of the outer cup-shaped layer. The inner peridium is globose and borne aloft as usual. When fully expanded the inner surface of the outer peridium has a white or flesh colored tinge, and under the lens is minutely granular. The inner peridium and area about the mouth is white, while the other portion is whitish or pale lead color. By the time the perforation appears at the center of the mouth the inner peridium is 2.5–3.5 mm in diameter and is sessile or only very slightly pedicellate.

The cup-shaped outer layer of the outer peridium is quite distinct and well formed, although it is quite firmly attached to the moss and bark and is very thin, the margin of course being split into a number of rays corresponding to the rays of the inner layer.

At my request Mr. J. M. Van Hook, assistant in the botanical department, photographed the plant, one photograph being taken with the plant enlarged two and one-half times to show more of the detail, while another photograph was taken natural size (*fig. 1*). The cup-shaped outer layer of the outer peridium, while intact, does not show very well in the photograph, because, being almost completely immersed in the moss, it could not be sufficiently lighted and brought into focus, though in one of the individuals, which was more or less removed from the moss, the outer layer being torn apart shows more distinctly.

The capillitium is white or pale yellowish, or pale yellowish-brown. It extends from the inner surface of the inner peridium toward the center. The threads are nearly straight, or very flexuous and irregular, the larger and more irregular ones being nearer the peridium. The threads are often flexuous and branched, but are sometimes unbranched for long distances. Their surface is smooth, except that it is often very irregular and more or less corrugated. They vary in diameter from 2–6 μ. The spores are very minute, 1.5–2.5 μ in diameter, white or very pale yellowish-brown, not echinulate nor tuberculate, many of them showing that they are more or less irregular and sometimes rather strongly angular.

FIG. 2.—Spores and threads of capillitium of *Geaster leptospermus*.

Dr. Coker has furnished me with an interesting note concerning the habitat and collection of the plant, which I append here:

"The plant was first found (a single specimen) by Mr. C. A. Shore, on the trunk of a cedar tree (*Juniperus virginiana*), growing with moss. Since that time I have found it repeatedly (as has also Mr. Shore) sometimes in large numbers (a score or more), and always on the trunks of trees growing with moss. It often occurs in association with *Lycoperdon leprosum* as the same situation is affected by both. The Geaster never grows in close clusters, but the individuals are scattered here and there at varying distances. It seems to grow indifferently on almost any tree where moisture conditions are favorable. I have found it on Ulmus, Hicoria and Juniperus. The mycelium penetrates the old bark and extends itself abundantly between the planes of cleavage."

The species may be described as follows:

Geaster leptospermus Atkinson & Coker, n. sp. Plants occurring singly or gregarious, oval to globose. Peridium 3–4.5 μ in diameter, outer layer closely attached to the moss and bark of the tree by numerous mycelial threads. Outer peridium splitting radially into 3–4 rays, its inner and outer layer then separated by a plane of cleavage, the inner layer being everted, leaving the outer layer in the form of a thin membranous cup with a stellate margin, points of the inner layer remaining attached to the points of the rays of the outer layer, its inner face minutely granular, white or with a flesh colored tinge. Inner peridium sessile or only very slightly pedicellate, 2.5–3.5 μ in diameter, globose and borne aloft by the eversion of the inner layer of the outer peridium, as in other fornicate species of the genus; mouth well defined, not sulcate nor striate, but marked by distinctly radiate silky threads, opening at maturity by a minute perforation; surface whitish or pale lead color, the area about the mouth white. Capillitium abundant, whitish or pale yellowish-brown, extending from the inner surface of the inner peridium towards the center; threads straight or very flexuous and irregular, simple or sometimes branched, 2–6 μ in diameter. Spores very minute, 1.5–2.5 μ in diameter, white or pale yellowish-brown, smooth, that is, not tuberculate nor echinulate, but often irregular and sometimes rather strongly angled, 3–4 angles in side view.

On moss covered dead bark of living trees (*Juniperus virginiana* Hicoria, Ulmus, etc.), woods, Chapel Hill, N. C.— GEORGE F. ATKINSON, *Cornell University, Ithaca, N. Y.*

TILLETIA IN THE CAPSULE OF BRYOPHYTES.

IT has been known for several years that the capsules of certain mosses and liverworts are sometimes attacked by fungous parasites that

fill these structures with a mass of mycelium, which develops small spores as in the Ustilaginales. These spores were first described for Sphagnum by Schimper in 1858 as "microspores," which he supposed to result from the extensive division of the spore mother-cells. Nawaschin, however, in 1892, determined the "microspores" to be derived from a fungus, which he regarded as probably a Tilletia and named *Tilletia* (?) *sphagni*. In the absence of information on the methods of spore germination, the exact position of the fungus must remain uncertain.

Cavers[2] has found a similar fungus in the capsule of *Pallavicinia Lyellii*, whose spores had also previously been called "microspores" by Warnstorf in 1887, and similar conditions were found in *Pallavicinia hibernica*. Cavers, however, presents no details of their structure and development.

The earliest observations on fungous mycelium in the liverworts seem to have been those of Leitgeb on several forms in the Jungermanniales.[3] He determined that the fungus entered the neck of fertilized archegonia and that the infected sporophytes, after a short period of irregular growth, remained abortive, the cavity becoming filled with mycelium in which spores were formed by abstriction.

The most recent contribution to the subject is by H. and P. Sydow[4] who have found this Tilletia-like fungus in the sporophyte of *Anthoceros dichotomus*, and named it *Tilletia* (?) *abscondita*. Nothing is known, however, of the development of this form.

Botanists are probably not generally aware that the liverwort, *Ricciocarpus natans*, harbors a parasite which appears to be similar to this Tilletia (?) described in the other bryophytes. I have repeatedly met it in the preparations of my classes where this liverwort was under observation. The infected capsules fail to mature and the interior becomes filled with small spores. These fungi offer an attractive field for investigation and their life history, completely studied, would clear up a very confused subject.—Bradley M. Davis, *The University of Chicago*.

[2] Cavers, On saprophytism and mycorhiza in Hepaticae. New Phytologist **2**: 30. 1903.

[3] Untersuchungen über die Lebermoose 2: —.

[4] Sydow, H. and P., Die Mikrosporen von *Anthoceros dichotomus* Raddi, *Tilletia abscondita* Syd. nov. spec. Ann. Mycologici **1**: 174–76. 1903.

TWO MEGASPORANGIA IN SELAGINELLA.

(WITH ONE FIGURE)

PROFESSOR BOWER records[5] finding two sporangia subtended by the same sporophyll of *Lycopodium rigidum*. In my work on *Selaginella rupestris* I have recently found two instances of the same irregularity. In both cases they were megasporangia, and were placed not side by

FIG. 1.—Longitudinal section of a megasporophyll of *Selaginella rupestris*, showing two megasporangia in nearly median longitudinal section. From a photomicrograph.

side as in the Lycopodium described by Professor Bower, but as if the additional sporangium was developed in the line connecting the normal megasporangium with the ligule, as shown in the figure. The two sporangia are of equal size, and no smaller than the other sporangia in the same cycle. The figure shows the normal reduction of the megaspores to one or two, so common in *Selaginella rupestris*, as recorded by the writer.[6]—FLORENCE M. LYON, *The University of Chicago.*

[5] BOWER, F. O., Note on abnormal plurality of sporangia in *Lycopodium rigidum* Gmel. Ann. Botany **17**: 278–280. 1903.

[6] BOT. GAZ. **32**: 138. 1901.

CURRENT LITERATURE.

BOOK REVIEWS.

Morphology of angiosperms.

THIS book,[1] which follows the one on gymnosperms by the same authors, seems a successful accomplishment of the authors' expressed purpose, "to organize the vast amount of scattered material so that it may be available in compact and related form." The want of such a book has long been felt by teachers, and several of the recently published accounts of research in this group make it evident that such a summing up of the facts and literature of the subject has been needed by investigators. The work is not merely a compilation, however, for much of the text, as well as the many pertinent figures credited to the authors, show that they themselves have worked over the subject-matter in many of its important phases.

In the introductory chapter are pointed out the differences between the gymnosperms and angiosperms, which, the authors believe, justify the raising of each of these groups to the rank of a grand division of the vegetable kingdom, as has been done by Warming and others. The close similarity shown by the monocotyledons and dicotyledons is given as sufficient reason for considering both groups together, in the discussion of each detail of development. The reviewer believes that the clearness, so characteristic of the book, could have been further enhanced by a separate treatment of each of these groups.

The discussion of the structure and development of the flower in chapter II is brief, but thoroughly modern, and it will doubtless serve a good purpose in helping to eradicate the older conceptions, still fostered in certain quarters by text-books and floras.

A detailed account of the phenomena of reproduction is given in six chapters (III–IX) with the following headings: microsporangium, megasporangium, female gametophyte, male gametophyte, fertilization, endosperm, and embryo. By the separate treatment of each of these phases of development the discussion gains much in lucidity and in convenience for reference.

The still debatable view of Strasburger that the gametophyte begins with the spore mother-cell, in which the characteristic reduced number of chromosomes first appears, is accepted by the authors. They hold that this view is supported also by the fact that in many temperate perennials the mother-cell stage is the one at which the seasonal rest in development occurs.

[1] COULTER, JOHN MERLE, and CHAMBERLAIN, CHARLES JOSEPH, Morphology of Angiosperms (Morphology of Spermatophytes, Part II). 8vo. pp. vii + 348. *figs.* 113. New York: D. Appleton & Co. 1903. $2.50.

The morphological individuality of the megasporangium is insisted upon, and the same claim is made for the sepal, petal, stamen, and carpel.

In the chapter upon the female gametophyte the development of this structure is followed up to fertilization, including the specialization of various parts of the embryo-sac as haustoria. The meaning of the constant occurrence of a definite number of chromosomes in each species is discussed, and also the criterion for distinguishing megaspore from megaspore mother-cell.

The chapter on the male gametophyte deals with the formation and germination of the microspore, and the reduction question. The authors hold that a qualitative reduction of chromosomes is not yet proven. The structures appearing in the pollen grain at germination they believe to represent an antheridium only, of which the pollen tube is the much elongated wall-cell.

In the discussion of fertilization, chalazogamy is thought to be an insufficient evidence of primitiveness. The centrosome is not demonstrated in angiosperms. "Double fertilization" is regarded a misleading name for the process so called, since this and all other nuclear fusions occurring in the embryo-sac probably differ profoundly from the fusion of the male nucleus with that of the egg.

In the chapter on the endosperm the various types of development of the part of the embryo-sac dominated by the endosperm nucleus are described. The endosperm is believed to be a renewed growth of the female gametophyte.

The specialization of parts of the proembryo and embryo for food absorption during development is emphasized in the chapter on the embryo. The characters of the cotyledons, it is held, cannot yet be considered as preponderating evidence in phylogeny. The chapter concludes with an account of parthenogenesis and polyembryony.

The reviewer believes that a valuable addition to the book could be made by following the chapters on endosperm and embryo with a thoroughly modern account of the germination of the seed.

A clear and suggestive résumé of our knowledge, and ignorance, of the interrelationships of the Monocotyledones, Archichlamydeae, and Sympetalae is contained in chapters X, XI, and XII.

Geographical distribution and fossil angiosperms are treated in the two following chapters. There is a concise and very useful summing up here of facts concerning these topics, which have been gathered from sources widely scattered and often inaccessible.

The facts of morphology assume definite relation and proportion only when they are built into some scheme attempting to express the phylogeny of the forms concerned. Such schemes of phylogeny are also the most useful indicators, to the investigator, of the forms most likely to yield important morphological results. If the scheme followed is erroneous, the worker is likely soon to discover the faults of the tool, and the refutation of a wrong

scheme of phylogeny is to be counted a step in advance, even though it be replaced by another imperfect one. The authors are, therefore, quite justified in giving the concise review and criticism of current views of the phylogeny of vascular plants that is to be found in chapter XV. Very important also, in its bearing on this subject, is the presentation of the leading facts of the anatomy of the vascular plants, given in the two concluding chapters of the book by professor Edward C. Jeffrey, of Harvard University.

The well arranged and efficiently complete bibliographies are sure to prove a most valuable feature of the book to investigators. An adequate series of figures has been well selected from many sources, and they are admirably executed, excepting perhaps the never-satisfying photomicrographs of the embryo-sac.—D. S. JOHNSON.

Experimental morphology.

THE LITERATURE of experimental morphology has received an important addition by Dr. Klebs. The present publication[2] is really a continuation of his older work (1896) on the physiology of reproduction in algae and fungi, and carries the theoretical as well as the experimental side of the subject of reproduction and development into higher plants. Beginning with a short history of the development of this branch of botany, from the time of Knight forward, the introduction proceeds with definition and discussion of such subjects as specific structure, causality, external and internal conditions, the teleological point of view, etc. As would be expected, this author does not regard a teleological explanation as any explanation at all. His clear exposition of the purely objective method of interpretation will doubtless be a great help to students who have difficulty in breaking away from the sometime prevalent teleology. His discussion of external and internal conditions is hardly satisfactory, however; one feels that, after all, the division, convenient as it may be, is an arbitrary one. Indeed, to the reviewer it seems as though we might soon be able to discard both terms altogether, naming a stimulus where we have come to know it and confessing ignorance where it is still outside our knowledge. A physiology based on study of the protoplasm can hardly make a distinction between external and internal factors; the cell-sap is physiologically as much external to the organism as is the atmospheric air, and the protoplasm itself is probably made up of a number of different systems, often external to one another, and influencing one another in many ways.

Klebs describes several new and instructive experiments with *Ajuga reptans*, *Glechoma hederacea*, *Veronica chamaedrys*, and others. By darkness, rather high temperature, and plenty of moisture, cuttings of the flowering shoot of *Ajuga reptans* were transformed into runners, producing rosettes instead of the normal floral bracts and flowers. Also, a runner submerged in water grows erect to the surface of the medium and then returns to its hori-

[2] KLEBS, G., Willkürliche Entwicklungsänderungen bei Pflanzen. pp. iv + 166. *figs. 28.* Jena: Gustav Fischer. 1903.

zontal habit. Flowering shoots of *Veronica chamaedrys* were made to take the form of an ordinary vegetative shoot by growing them as cuttings in moist air. Many other fascinating experiments are described.

The book is full of suggestive theoretical discussions. In the author's interpretation of these phenomena of higher plants, the responses already obtained in lower plants are taken into account. Thus, the whole manner of treatment is one based on the physiology of the cell itself. On the whole, the work is an admirable one and one which will immediately take its place alongside Dr. Klebs's earlier treatise as among the first to present the subject of development from the standpoint of objective physiology.—BURTON E. LIVINGSTON.

MINOR NOTICES.

THE THIRD PART of Maiden's Revision of the genus Eucalyptus[3] contains text and figures for *Eucalyptus calycogona* Turcz.—C. R. B.

THE SIXTEENTH PART of Engler's *Das Pflanzenreich* includes a conspectus of the families Scheuchzeriaceae, Alismataceae, and Butomaceae by Fr. Buchenau.[4]—C. R. B.

"WITH THE TREES"[5] is the title of a recent book which furnishes evidence of the increasing popular interest in the trees and forests. Such subjects as: When the sap stirs, The life of leaves, The work of leaves, In the high woods, In a hillside pasture, Trees of streets, parks, and gardens, are very interestingly treated by the author. The book indicates a thorough knowledge and familiarity with the botanical problems discussed. The usual tendency of popular writers to personify plants is carried to an extreme in many cases. While this may lend a certain vivacity to the style, the practice is unfortunate, because it conveys erroneous impressions of the life-processes and of the probable origin of structures in plants. The book is very well illustrated from photographs by Edmund H. Lincoln and C. B. Going.—CLIFTON D. HOWE.

THE STUDY of the life-history of truffles has lately engaged the attention of several French investigators. On December 10, 1900, M. Émile Boulanger deposited with the Paris Academy of Science a sealed paper, which was opened at his request on May 4, 1903. It contained a description of his success in germinating the ascospores of *Tuber melanosporum* and *T. uncinatum*. He further described the mycelium, and a conidial stage, and announced

[3] MAIDEN, J. H., A critical revision of the genus Eucalyptus. Part III. pp. 77–90. *pls. 9–12*. Published by the Government of the state of New South Wales. Sydney: W. A. Gullick. 1903. *2s. 6d.*

[4] ENGLER, A., Das Pflanezenreich. Heft 16. Scheuchzeriaceae (pp. 19), Alismataceae (pp. 66), und Butomaceae (pp. 12), von Fr. Buchenau. Leipzig: Wilhelm Engelmann. 1903. *M.* 5.

[5] GOING, MAUD, With the trees. 12mo. pp. x + 335. *figs. 40*. New York: The Baker and Taylor Co. 1903. $1.00.

his plans for cultivation of these species on a considerable scale in the open. M. Louis Matruchot later presented a note to the Academy of Sciences in which he announced for the mycelium of these truffles characters absolutely contrary to those given by M. Boulanger. M. Boulanger has now published a quarto pamphlet,[6] figuring and describing the germination of the ascospores *Tuber melanosporum*, in which he also has reprinted extracts from the proceedings of the Academy of Sciences and the Bulletin of the Mycological Society of France, of various dates. From the description which he gives and the terminology used it would appear that he is absolutely unqualified by a knowledge of the morphology of fungi to discuss the recondite matters upon which he is engaged.—C. R. B.

IN BULLETIN 44 of the Bureau of Plant Industry, von Schrenk and Spaulding[7] give an excellent account of the bitter rot, which is one of the most serious enemies of the apple industry in the middle states. The bulletin deals first with the disease as it appears on the fruit, and later with the canker stage, which is shown to arise from the infection of wounds by spores, and to enable the fungus to live through the winter. Both phases are illustrated by numerous excellent half-tone engravings. The growth of the fungus in cultures is also treated. In describing the germination of the spores the authors follow the error of many other writers in regarding the appressoria as some kind of "chlamydospore."

From the historical review it appears that the bitter rot fungus has been described under various names on grapes, apples, peaches, and nectarines. Recently the ascus-form of several anthracnoses has been discovered. Those species were separated as a genus, *Gnomoniopsis* Stoneman. Since this name had been previously used, the authors propose the name Glomerella[8] for all anthracnoses whose ascus-form is known. The bitter rot fungus, through synonymy, becomes *Glomerella rufomaculans* Spaulding and von Schrenk. The paper concludes with a very comprehensive bibliography.—H. HASSELBRING.

THE SUCCESS of Dr. Grout's little book *Mosses with a hand lens*, has led him to publish a new and larger work,[9] of more extended scope. Even this makes no pretensions to being a complete manual, but is intended rather to attract and help students who would otherwise never begin the study of

[6] BOULANGER, M. ÉMILE, Germination de l'ascospore de la truffe. pp. 20. *pls.* 2. Paris. 1903. Apparently published by the author.

[7] VON SCHRENK, H., and SPAULDING, P., The bitter rot of apples. Bull. no 44. Bureau of Plant Industry. U. S. Dept. of Agric. pp. 54. *pls.* 9. *figs.* 9. 1903.

[8] Also published in Science N. S. **17**: 75. O 1903.

[9] GROUT, A. J., Mosses with hand lens and microscope, a non-technical handbook of the more common mosses of the northeastern United States. Part I. Imp. 8vo. pp. i + 86. *pls.* 10. *figs.* 35. Brooklyn, N. Y., 360 Lenox Road: Published by the author. 1903. $1.

mosses. Inasmuch as the diagnostic characters of the species are drawn chiefly from the author's experience, every student of mosses may find the book not only convenient for the ready determination of miscellaneous collections, but even helpful in discriminating critical species. Half of the first part is devoted to directions for collecting, preserving, mounting, methods of manipulation, an account of life history and structure, and an illustrated glossary of bryological terms. The beginning of the manual proper occupies the remainder, with descriptions of Sphagnaceae, Andreaeaceae, Georgiaceae, Polytrichaceae, Buxbaumiaceae, Fissidentaceae, and Dicranaceae. The descriptions of families are rather full, the classification following closely Jameson's *Handbook of British Mosses*, and they are accompanied by numerous illustrations of the characteristic structures. Many of the plates are reproduced from the *Bryologia Europaea*, some from Sullivant's *Icones Muscorum*, while a goodly number of illustrations are original. The book deserves hearty welcome from teachers and students.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS.

ATTENTION SHOULD BE CALLED to an important article by F. Cavers[10] on asexual reproduction and regeneration in Hepaticae. The paper supplements the extensive work of Correns on similar phenomena in the mosses.—C. R. B.

MR. W. C. W[ORSDELL] writes a historical sketch[11] of the phenomenon of "double fertilization" in angiosperms in which most of the literature of the subject is mentioned except the work of American students, and this is conspicuous by its absence.—C. R. B.

DR. EMERICH ZEDERBAUER holds[12] that two of the Myxobacteriaceae described by Thaxter, *Myxococcus incrustans* and *Chondromyces glomeratus*, and probably all members of the group, are compound organisms, like lichens, a true fungus on the one hand in symbiosis with a bacterium on the other. He has grown each component separately in pure cultures and studied their characteristics.—C. R. B.

M. PH. EBERHARDT has made an extended study of the influence of dry air and humid air upon the form and structure of plants.[13] The work was carried on at the botanical laboratory of the Sorbonne and the experimental grounds at Fontainebleau. Plants growing in the ground were covered with

[10] CAVERS, F., Asexual reproduction in Hepaticae. New Phytologist **2**: 112–133, 155–165. *figs. 8.* 1903,

[11] W[ORSDELL], W. C., The phenomenon of "double fertilization" in angiosperms; an historical sketch. New Phytologist **2**: 145–155. 1903.

[12] ZEDERBAUER, EMERICH, Myxobacteriaceae eine Symbiose zwischen Pilze und Bacterien. Oesterr. Bot. Zeits. **53**: 309. 1903.

[13] EBERHARDT, PH., Influence de l'air sec et de l'air humide sur la forme et sur la structure des végétaux. Ann. Sci. Nat. Bot. VIII. **18**: 61–153. *pl. 1.* 1903.

bell jars of adequate size, proper arrangements being made for ventilation and for maintaining the moistness or dryness of the air at will. Although the paper contributes few entirely new facts, it brings experimental evidence to bear upon conclusions already drawn from comparative observations.—C. R. B.

SCHIFFNER'S studies[14] of Gymnomitrium and Marsupella may be summarized in the following synonymy: MARSUPELLA SPRUCEI (Limpr.) Bern. *stat.* MARSUPELLA USTULATA Spruce (*Sarcoscyphus Sprucei decipiens* Limpr.; *Nardia gracilis* Mass. & Car.). GYMNOMITRIUM ADUSTUM Nees (*Marsupella olivacea* Spruce; *Acolea brevissima* Dum. inadmiss.). MARSUPELLA CONDENSATA (Angstr.) Kaal. (*Gymnomitrium condensatum* Angstr., *non* Limpr.; *Sarcoscyphus aemulus* Limpr., *et auct.*) MARSUPELLA (*Hyalacme*) APICULATA Schiffn. (*Gymnomitrium condensatum* Limpr. *et auct., non* Angstr.). GYMNOMITRIUM ALPINUM (Gott.) Schiffn. (*Sarcoscyphus alpinus* Gott.)

BY USING MODERN METHODS in an investigation of the development of the antheridial "flower" of Polytrichum and Mnium, Vaupel seems to have settled the Hofmeister-Leitgeb-Goebel controversy as to its morphology.[15] In Mnium each cluster of antheridia in the "compound male flower" (*i. e.*, each twig of the branch system) corresponds to the antheridial group of Funaria, in that the first antheridium develops from the apical cell, the rest arising at various points. Leaf formation in the center of the "flower," however, is suppressed, all the segments forming antheridia. But in Polytrichum the apical cells of the twigs do not produce antheridia, persisting even until rudiments of the last antheridia appear. Thus again the truth lies between the contestants. Vaupel also ascertained that the brown substance in certain cells of the paraphyses of *Mnium cuspidatum* and *Polytrichum juniperinum* prevents the absorption of water by the stems, leaving it all to the antheridia; that the opening of the antheridia of Marchantia is due to the swelling of the mucilage laid down in the wall cells; and that the rhizoid strands of Polytrichum are primarily water conductors.—C. R. B.

RESPIRATION.—Further researches on the influence of injuries upon the respiratory quotient have been made by Maximow,[16] who corrects some of Richards's results, confirms others, and concludes that (1) the variations are due partly to the capacity of fleshy organs to retain for a time considerable amounts of CO_2 and to eliminate it later in excess; (2) when injured the early increase of CO_2 (which soon ceases) is due to the exposure of additional

[14] SCHIFFNER, VICTOR, Studien über kritische Arten der Gattung Gymnomitrium und Marsupella. Oesterr. Bot. Zeits. **53**: 95–99, 166–172, 185–194, 246–252, 280–284. *pls. 2–4.* 1903.

[15] VAUPEL, F., Beiträge zur Kenntniss einiger Bryophyten. Flora **92**: 346–370. 1903.

[16] MAXIMOW, N. A., Ueber den Einfluss der Verletzungen auf die Respirationsquotient. Ber. Deutsch. Bot. Gesells. **21**: 252–259. 1903.

free surface; (3) the value of the respiratory quotient then falls rapidly, sometimes as low as 0.5, reaching a minimum before respiratory activity attains its maximum, which it does on the second or third day; (4) with healing, normal conditions again gradually prevail.

NABOKICH confirms[17] earlier results of Polowzoff[18] that a considerable part (25–50 per cent. of the CO_2 usually ascribed to the respiration of seeds in experiments is really due to the respiration of microorganisms, as shown by a comparison of the respiration of sterile and infected seeds. He also ascertained that the antiseptics used (bromin and corrosive sublimate) did not depress the respiration of the seeds, but clearly accelerated it.—C. R. B.

[17] NABOKICH, A. J., Ueber den Einfluss der Sterilisation der Samen auf die Athmung. Ber. Deutsch. Gesells. **21**: 279–291. 1903.

[18] POLOWZOFF, W. W., Untersuchungen über die Athmung der Pflanzen. Ber. Kaiserl. Akad. Wiss. VIII. **12**: 14–16. 1903.

NEWS.

DR. WILLIAM TRELEASE spent a month in Mexico this summer in the study of agaves and other plants.

DR. O. MELVILLE BALL, of Batesville, Va., and DR. E. F. FRITSCH, of London, have been elected members of the German Botanical Society.

MR. W. BOTTING HEMSLEY, keeper of the Kew Herbarium, has been made associate editor (with Sir Joseph Hooker) of the *Botanical Magazine*.

THE BOTANICAL DEPARTMENT of Stanford University has just entered the new and commodious quarters which have been in process of construction for more than three years.

DR. J. A. HARRIS, of the Missouri Botanical Garden, has been appointed assistant in the Shaw School of Botany of Washington University. An appointment of his successor at the Garden will shortly be made.

MR. CHARLES A. DAVIS, instructor in forestry in the University of Michigan, is engaged in an extended comparative study of the inland lakes and bogs of the lower peninsula of the state with reference to their geological and botanical history and the conditions of peat formation.

PROFESSOR CHARLES E. BESSEY has been accompanying his son this summer in a journey through the Caucasus region. They crossed the mountains by the Mamisson pass—"a botanist's paradise," he writes—and were in Tiflis on August 19. After a week's journey to the south, they were to turn homeward.

MR. FILBERT ROTH, recently appointed to the chair of forestry in the University of Michigan, has also been elected forest warden of the state by the Michigan Forestry Commission. He has organized a party of forestry students, who are engaged in a preliminary survey of the state forest reservations in Roscommon county, Michigan.

WE LEARN from the *Journal of Botany* that the second and third volumes of the *Icones ad Floram Europae*, including plates 281–500, have been issued under the superintendence of M. Camille A. Jordan, the text having been prepared by the late Alexis Jordan. The remaining incomplete text and about 100 plates will not be published, but have been intrusted to the Botanical Society of France, at whose rooms they may be consulted.

DR. D. H. CAMPBELL left San Francisco on May 15, spent three weeks in New Zealand, and a month in Australia, where, through the kindness of Mr. Maiden, the director of the Sydney Gardens, he saw a great deal of the very

characteristic flora of the country, going as far as Melbourne and a little north of Brisbane, besides making a number of shorter excursions. On the the way back he was two weeks in Hawaii, returning to Stanford University September 1.

DR. HERMAN VON SCHRENK, whose government work has been growing constantly, withdraws from the School of Botany of Washington University to give all of his time to the work in plant pathology and the preservation of timbers for the Department of Agriculture, with the title of Chief of the Division of Forest Products, under the Bureau of Forestry. He continues in charge of the Mississippi Valley Laboratory of the Bureau of Plant Industry, located at the Missouri Botanical Garden.

A GARDEN OF MEDICINAL PLANTS is to be established at Golden Gate Park, San Francisco, Cal. The park commissioners have set aside eight acres of ground in a well protected part of the park and have instructed the park superintendent and the authorities of the California College of Pharmacy to further the plans of such a garden. Climatic and other conditions are exceptionally favorable, and it is believed that fully 90 per cent. of all medicinal plants may be grown in the open. Others will be cared for in greenhouses.

AT THE UNIVERSITY OF IOWA: Men have been in the field all the year making collections to complete as far as possible the herbarium representing the state flora. Collections have been made chiefly in the northeastern and in the southern counties of the state. PROFESSORS MACBRIDE and SHIMEK have just returned from an excursion down the valley of the Rio Grande. They bring back large collections both of cryptogamic and flowering plants, besides a very large number of photographs representing the ecological conditions of mountain and plain, forest and desert.

AT THE UNIVERSITY OF CALIFORNIA: PROFESSOR W. A. SETCHELL is spending his sabbatical year in journeying around the world. His time is to be devoted mainly to botanical sightseeing.

PROFESSOR W. L. JEPSON, who is acting head of the department of botany in the absence of Professor Setchell, has devoted the last two summers to a field study of the forests of northwestern California, centering his investigations particularly on the tan oak and the tanbark industry.

Mr. H. M. HALL, who has charge of the herbarium, which now contains 50,000 sheets, made a wagon journey this summer through the cañon of the upper Sacramento River, circled Mount Shasta, crossed the Modoc lava beds, passed south to Larsen Peak, and threaded the Sierra Nevada Mountains to the Tahoe region and the Calaveras grove. It was a long and very productive journey.

SIR THOMAS HANBURY has presented to the Royal Horticultural Society of London a tract known as Wisley Garden, situated twenty miles from Hyde Park Corner. The *Gardener's Chronicle* reports it as "unique . . . . devoid

of all plan and in all its aspects as wild as a garden can be . . . . It was made piecemeal and as the late Mr. Wilson's fancy dictated. . . . . There are no broad paths . . . . no geometrical beds. . . . . All is natural, yet natural with plants of every conceivable description. . . . . Not a thing is named, but labels in such a garden, if used, must be numbered by thousands. . . . . There is no digging permitted in the many acres thus wildly planted. The men do little else but pull weeds, and occasionally use the knife." It is to be hoped that the garden will be maintained as at present and that the Society will reorganize its garden at Chiswick and equip it with a staff of investigators for experimental work.

NOTES FROM THE BUREAU OF PLANT INDUSTRY OF THE U. S. DEPARTMENT OF AGRICULTURE:

DR. GEORGE T. MOORE, physiologist, has been sent to Europe for the purpose of investigating the methods used there in the study of soil bacteriology, and for the purpose of securing plants of various kinds for the Office of Seed and Plant Introduction. He will return in January.

MR. W. T. SWINGLE has just returned from the Mediterranean region, after an extended study of the pistache, a nut-bearing tree which the department is introducing into the southwest. Mr. Swingle has also made a careful study of several other Mediterranean crop plants and fruit trees, which the department is proposing to introduce into the same region. He will remain in Washington for some time.

MR. P. H. DORSETT has been authorized to establish in some portion of southern California a plant testing and acclimatization garden, in cooperation with the Agricultural Experiment Station of California. This garden will be used to test and propagate rare and valuable plants introduced by the department. MR. W. W. TRACY will assist Mr. Dorsett in selecting the location, which will be announced soon.

MR. W. M. SCOTT, late state entomologist of Georgia, will give his attention especially to work on the diseases of orchard fruits.

A NUMBER of scientific assistants and aids have recently been appointed. In the Office of Physiological and Pathological Investigations: P. J. O'GARA, GEORGE F. MILLS, LEONARD F. HARTER, of Nebraska, and ARTHUR H. LEIDIGH, of Kansas. Mr. O'Gara and Mr. Harter will be stationed in Washington, and Mr. Leidigh at Amarillo, Texas, on one of the government experiment farms. In the office of the agrostologist: M. A. CROSBY, and M. B. STEVENS, of Michigan; BYRON HUNTER, of Washington; R. A. OAKLEY, of Kansas; C. W. WARBURTON, of Iowa.

MR. W. J. SPILLMAN is investigating forage conditions in the northwest. C. R. BALL and DAVID GRIFFITHS are also in the field, the former in connection with the exhibits at St. Louis, and the latter studying range problems in the southwest.

MR. A. S. HITCHCOCK has returned from a three-months' trip from Louisiana to California and Washington, where he has been investigating

agricultural conditions, and the methods for preventing the drifting of sand in sand-dune areas. MR. J. M. WESTGATE, a graduate of the Kansas Agricultural College and later a student in the botanical department of the University of Chicago, has been appointed an assistant in this work.

MR. C. V. PIPER, professor of botany in the Washington Agricultural College, has been appointed systematic agrostologist in charge of the herbarium of grasses.

PROFESSOR L. H. BOLLEY is still in Russia, studying varieties of flax with a view to introducing desirable kinds into the United States. He will return about November 1.

MR. J. E. W. TRACY is in Europe studying the seed-growing industry. He will make himself familiar with the methods of the best growers and with the most desirable new European varieties of vegetables.

THERE WILL soon be published as a bulletin a paper entitled "Conditions influencing the vitality and germination of seeds," by DR. J. W. T. DUVEL. It is a historical review of the work already done on the vitality of seeds, as well as a report of the results of his own investigations carried on at the University of Michigan in 1900, 1901, and 1902.

MR. ERNST BESSEY is at present in the Caucasus making observations on such of the native fruits and nuts as may seem valuable, and will send seeds and plants to the United States.

MR. GEORGE OLIVER has just returned from Florida, where he studied the mango culture with a view to the further introduction of choice varieties.

MR. BARBOUR LATHROP, of Chicago, who has made several expeditions at his own expense to different parts of the world, in search of valuable seeds and plants for introduction into America, has just returned. He has employed on his various expeditions MR. D. G. FAIRCHILD, who now resumes his connection with the department as one of its agricultural explorers. The countries visited this year with a view to more thorough exploration later by the department agents were Italy, Sicily, Tripoli, Tunis, Malta, Egypt, German East Africa, Zanzibar, Portuguese East Africa, Natal, Transvaal, Cape Colony, Grand Canary, Madeira, Portugal, Spain, Bohemia, Sweden, Denmark, Holland, Belgium, and England. Such seeds and plants as were secured were given by Mr. Lathrop to the Department of Agriculture for propagation and distribution, and it is hoped that some of them may prove of great value to the country, repaying him for his patriotic and generous interest in increasing the variety of food and ornamental plants of America.